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THE SYSTEMATICS AND EVOLUTION OF *EPILOBIUM* (ONAGRACEAE) IN SOUTH AMERICA¹

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ABSTRACT

Recent field, cytological, experimental hybridization, and morphological studies indicate that the patterns of diversity in South American species of *Epilobium* can best be understood by recognizing 12 native species. These have been derived from at least five independent pre-European introductions of *Epilobium* into South America, with subsequent diversification in some of these lines. Two groups have ancestral affinities with North America: *Epilobium ciliatum* ssp. *ciliatum* is consubspecific with North American populations; the primarily northern Andean group, consisting of *E. denticulatum* and allied species, has no close relatives in the Northern Hemisphere, but has a chromosomal arrangement identical with that of some North American species. Two other lines are derived directly from Australasian ancestors: *Epilobium hirtigerum* is conspecific with a widespread species of Australia and New Zealand, and *E. conjungens*, with its unusual creeping habit and consistently opposite

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leaves, is closely allied to *E. brunnescens* ssp. *brunnescens* of New Zealand. Progenitors of these species presumably arrived by long-distance dispersal via the prevailing westerlies. The remaining species are southern South American, and show no close affinities with species found in other geographical areas. Fertility data from experimental hybrids suggest a close alliance between some of the morphologically distinct species in this group. Their precise relationships, however, and the origin of possible ancestors, remains obscure, although Australasia appears to be the most likely source. Three other species have been introduced into South America in historical times, two from Europe and one from North America.

Epilobium, the largest genus in the Onagraceae, comprises approximately 185 species distributed worldwide in temperate zones on every continent except Antarctica. In tropical regions the species are restricted to temperate montane habitats. Many species are extremely variable and widespread, while others are highly restricted. In general, the genus has been characterized as "taxonomically difficult."

During the last 20 years, a steadily growing number of papers have been published that provide modern treatments for the species of *Epilobium* encountered in Europe (Raven, 1968), Africa (Raven, 1967b), parts of western Asia (Chamberlain & Raven, 1972; Raven, 1964) and eastern Asia (Hara, 1965; Raven, 1962, 1967a), Australasia (Raven & Raven, 1976), and North America (Munz, 1965; Hoch & Raven, 1981b). With the exception of some large parts of continental Asia, the only region without a recent treatment is South America.

Prior to the present study, the only papers dealing specifically with *Epilobium* in South America were those by Samuelsson (1923, 1930). Carl Haussknecht (1884) produced a monograph of worldwide scope, which is still the only comprehensive treatment available. Samuelsson discussed a species only when new specimens amplified or diverged from the limits given by Haussknecht; he described new taxa based on new interpretations of morphology or material collected since Haussknecht's time. In several places Samuelsson pointed out the difficulty of separating some of the taxa he recognized, including some of his new ones, and this suggested that there were a number of taxonomic problems among the South American species of this genus.

Since the early 1920s a substantial quantity of new herbarium material has become available, amounting to many times more than Samuelsson had for study. During these same intervening years, there have been fundamental changes in our concept of the kinds of units that should be regarded as species. A reassessment of the South American species of *Epilobium* in the light of these concepts was viewed as necessary to bring the species into conformity with the approach and philosophy used by Raven & Raven (1976) and Hoch (1978).

Equally important are recent chromosomal studies (Seavey, 1972; Seavey & Raven, 1977a, 1977b, 1977c, 1978; Hair, Raven & Seavey, 1977), especially a preliminary survey of South American plants (Seavey & Raven, 1977c), in which it was suggested that, based on morphology and the distribution of chromosomal end arrangements, the *Epilobium* species in South America may have been derived from ancestors from both North America and Australasia. In order to understand the implications of this interesting biogeographical problem, it was first necessary to delimit taxa that were present in South America. Once the taxa were

circumscribed, additional studies would provide some understanding of the interrelationships among them.

The following questions were kept in mind as this study progressed: How many taxa would it be useful to recognize? Did populations exhibit morphological patterns that had a geographical basis or did the same patterns appear numerous times in different areas? Are the taxa sympatric; do they hybridize, and, if so, what role has hybridization played in the differentiation of natural populations? Where did the taxa originate? What is their relationship with each other, and what impact did historical/geological processes have on their evolution and current distribution? An attempt has been made to answer these questions in greater or lesser detail, depending on the data that could be brought to bear on the subject.

MATERIALS AND METHODS

An extensive field examination was made of hundreds of populations in the central and southern Andes of Argentina and Chile, and in the altiplano of Bolivia. To supplement the field observations, nearly all of the available herbarium specimens representing the genus in South America were studied.

Seeds collected in the field, from herbarium specimens, or provided by correspondents, were grown in greenhouses at the Missouri Botanical Garden for observation. All plants grown from a single seed source, which may be one or more plants from one collection, are here defined as a strain. Many strains were used in making additional experimental hybrids to expand the studies reported by Seavey & Raven (1977c). These were examined cytologically. Buds were fixed in 1:3 acetic alcohol, hydrolyzed in 1 N HCl for 10–15 minutes at 60°C, stained in acetocarmine and squashed for chromosome observations. In addition, a measure of pollen fertility in the experimental hybrids and suspected natural hybrids was obtained using the malachite green-acid fuchsin-orange G stain of Alexander (1969). Two buds (or flowers, if buds were unavailable) were selected from each plant, pollen from each bud was stained and 100 tetrads scored for aborted and nonaborted grains. The scores for filled grains from the two buds were averaged to give a percentage of stainable pollen for each plant. Generally, two or more individuals of each artificial hybrid strain were averaged to arrive at the figures presented. In some instances, if only one bud was available, the percentage for that bud alone was used, or if there was a striking disparity between the two scores, the higher one was used, since it represents a potential fertility under good conditions.

GENERIC RELATIONSHIPS

Epilobium is one of two genera currently recognized in the tribe Epilobieae. This tribe differs significantly from the six other tribes of the family Onagraceae in that it has minute, heteropycnotic chromosomes (Kurabayashi et al., 1962); sheds pollen, in most species, as tetrads; has gametic chromosome numbers of $n = 9, 10, 12, 13, 15, 16, 18,$ and 19 , and multiples of some of these numbers; and occurs primarily in moist or seasonally moist habitats (Raven, 1976).

In addition to *Epilobium*, Epilobieae contains the genus *Boisduvalia*, which is represented in western North America by five species, one of which is shared with South America, and a sixth species endemic to South America (Raven & Moore, 1965). Although *Boisduvalia* is clearly closely related to *Epilobium*, it differs in having an annual habit (only three species of *Epilobium* are annual); angular-fusiform seeds without a terminal coma (Seavey et al., 1977); and chromosome numbers of $n = 9, 10, 15$, and 19 . Only $n = 15$ is shared with five species of *Epilobium*, but they have been derived independently of *Boisduvalia* (Raven, 1976).

Epilobium itself is clearly delimited, although two genera, *Zauschneria* and *Chamaenerion*, are often segregated from *Epilobium*. Including these groups, *Epilobium* consists of six well defined sections (Raven, 1976). Section *Cordylorum*, with three species, and sect. *Zauschneria*, with two, are closely related, share a number of morphological features, and have a base chromosome number of $x = 15$. Polyploidy is known in some subspecies of *E. canum* (Greene) Raven (sect. *Zauschneria*). Two other sections contain the only annual species in the genus, two in sect. *Crossostigma* and one, *E. paniculatum* Nutt. ex Torr. & Gray, in sect. *Xerolobium*. These sections are characterized by unusual morphologies and the chromosome numbers, $n = 13$ or 16 and $n = 12$, respectively. The center of distribution for these four sections lies in western North America. A fifth, very distinctive, group is sect. *Chamaenerion*. Unlike the preceding four sections, the center of distribution for the seven species of sect. *Chamaenerion* is in Eurasia, with only two, *E. angustifolium* L. and *E. latifolium* L., occurring in North America. Section *Chamaenerion* has a base chromosome number of $x = 18$, with polyploids known only in *E. angustifolium* and *E. latifolium*.

The sixth section, sect. *Epilobium*, accounts for the bulk of the genus. The five sections enumerated above contain only 15 species out of a total of approximately 185, leaving about 170 in sect. *Epilobium*, all of which have a gametic chromosome number of $n = 18$. These are widely, but unevenly, distributed in moist, open habitats throughout the temperate regions of the world. For example, Eurasia has more than 70 species, but Africa has only 11, with seven of these shared with Eurasia. There has been a remarkable radiation of this section in New Zealand unparalleled elsewhere in the world, resulting in 37 species, of which 31 are endemic and the remainder shared with Australia. The most primitive member of sect. *Epilobium*, *E. rigidum* Hausskn., is found in western North America, where four of the other sections are also restricted. This pattern of distribution, along with the great morphological and chromosomal diversity exhibited by these sections, leads to the conclusion that *Epilobium* probably originated in western North America (Raven, 1976).

The native South American species are all members of sect. *Epilobium*. In the present treatment 12 native species are recognized. These are distributed along the length of the Andes from Costa Rica, northern Venezuela and Colombia to Cape Horn, except for *E. hirtigerum*, which is restricted to eastern Argentina, Uruguay, and southern Brazil. The greatest concentration of species is found in the central and southern Andes of Argentina and Chile. In addition, three other species have been introduced and persisted or become naturalized in historical times. *Epilobium obscurum* and *E. tetragonum* subsp. *lamyi*, from Europe, are also

members of sect. *Epilobium*. The third species, *E. paniculatum* (sect. *Xerolobium*) has been introduced from North America. A fourth species, *E. angustifolium*, representing sect. *Chamaenerion*, has been collected once in Chile (Valdivia, Valdivia Prov., Chile, Calvert in 1914, BM). If this specimen is correctly labeled, then the plant was probably cultivated and has failed to persist or become naturalized. In the absence of additional information, it has been excluded from further consideration.

Hausknecht (1884) grouped the species of *Epilobium* into assemblages based on stigma lobing, seed shape, and other conspicuous morphological features. Samuelsson (1923) maintained these groups for the South American species as outlined by Hausknecht and created two additional ones by removing the taxa allied to *E. australe* from the *Platyphylla*, placing them in his *Australia*, and by segregating *E. nivale* and *E. fragile* as *Nivalia*. Although Hausknecht's categories did bring together species of similar morphologies, the arrangement of the groups and some of their component species do not reflect our current understanding of the genus. Until a much more detailed understanding of the reticulate morphological patterns seen in sect. *Epilobium* is acquired, it does not seem warranted to recognize any assemblages such as those proposed by Hausknecht.

MORPHOLOGY

In dealing with the South American species of *Epilobium* sect. *Epilobium*, a variety of morphological characters have been useful in delimiting the species, especially habit, perennating structures, pubescence, leaf shape, dentition and arrangement, and seed shape and surface features.

Habit. *Epilobiums* in South America exhibit a diverse array of habit and growth form. Some species have erect or ascendent stems (e.g., *E. ciliatum*, *E. glaucum*); others are lax or decumbent (*E. nivale*), and often caespitose (*E. densifolium*, *E. fragile*, *E. nivale*). Perhaps the most unusual growth form is that of creeping stems, rooting along their length and with flowers arising from subterminal nodes, characteristic of *E. conjungens*. This habit is shared only with a number of species from Australasia (Raven & Raven, 1976).

All the species in sect. *Epilobium* are perennial herbs. They produce a variety of perennating parts for vegetative reproduction and persistence during the winter. All of the South American species will germinate, flower, and set seed during a single growing season, so it is potentially possible for them to be facultatively annual. This does not, however, seem to be an important factor except, perhaps, in those species that show the greatest tendency to weediness (e.g., *E. ciliatum*).

There are very great differences in branching patterns, from simple to profusely branched. This trait is so variable within species or even populations, however, and so strongly influenced by the age of the plant and the microclimatic conditions under which it grows, that it is of little taxonomic value.

In the Northern Hemisphere, a wide variety of highly specialized perennating structures has evolved, including compact underground buds with fleshy, imbricate cataphylls (turions), leafy rosettes, rhizomes, corms at the tips of thin stolons, and leafy soboles or shoots. Only *Epilobium ciliatum*, of the native South American species, produces turions or leafy rosettes, usually toward the end of

a growing season. In general, the other species are less specialized in this respect, reproducing vegetatively by buds at or near the ground surface or by more or less elongated leafy shoots from the bases of the stems. The leafy shoots in *E. barbeyanum* often take the form of runners 20 cm or more long. Two species, *E. australe* and *E. glaucum*, produce short or elongate scaly rhizomes just under the ground surface, which, in the case of *E. glaucum*, may be up to 20 cm long. These various modes of perennation generally result in clumped groups of stems, although solitary, single-stemmed individuals can be found in many species. *Epilobium ciliatum* is usually solitary, since each plant produces only one or two turions or rosettes, which give rise to the following year's plant. As previously mentioned, *E. conjungens* is quite unusual among the South American species. Its stems form small mats of repent branches, a habit that has apparently evolved through the suppression of the main shoot with a concomitant proliferation of basal shoots (Raven & Raven, 1976).

A conspicuous feature of two of the clumped, caespitose species, *E. densifolium* and *E. fragile*, is the thick, woody, often elongate rootstock. This is in striking contrast to the normally fibrous root system produced by other species.

Pubescence. There are four basic types of hairs found among the species under consideration. The presence or absence of each type has been very useful, either alone or in combination with other characters, in separating taxa. Two species, *E. glaucum* and *E. nivale*, are conspicuous by the absence of pubescence of any type, and the often blue-glaucous, waxy bloom in the former. Very rare glabrous individuals of *E. ciliatum* have been seen, but normally this species is pubescent.

1. Strigillose. Hairs of this type are sharp-pointed, appressed, or at least falcate, upwardly curved, and typically 0.1–0.2 mm long. Following Raven & Raven (1976) and Hoch (1978), these hairs have been termed strigillose. This is by far the most common pubescence type found in *Epilobium*. The density and distribution of strigillose hairs varies considerably within and between species, but they are found in nearly all species except for the glabrous ones mentioned above. There is some variation in how closely appressed the strigillose hairs are on an individual plant. Often the hairs on the ovaries are closely appressed, while those elsewhere on the plant are more spreading.

In *E. puberulum* the basic strigillose hair type is generally longer, ranging from 0.15 to 0.4 mm, and often somewhat spreading. A second modified hair type occurs in *E. conjungens*. In this species the hairs are much smaller, 0.02–0.08 mm long, and often curled in dried specimens. It is not known if these hairs are straight in living plants, but because they are distinctive, this type of pubescence has been termed puberulent.

2. Glandular. These hairs are more or less appressed to erect, blunt-tipped, 0.1–0.2 mm long. In living plants each hair usually exudes a minute droplet of liquid. When they are sufficiently abundant, as in *E. barbeyanum* and some populations of *E. ciliatum*, the entire plant may feel moist or viscid to the touch. Normally, when dried, these hairs become flat and twisted with an evident rounded tip. Glandular hairs are absent in *E. australe*, *E. densifolium*, *E. puberulum*, and *E. conjungens*. In the other species their density and distribution vary con-

siderably, but they are generally present in the inflorescence, on the ovaries and floral tube, and along the margins of young leaves.

3. Long, erect. A distinction is made here between two types of erect hairs that are each restricted to a single species. The long, very fine, soft, erect hairs found in *E. hirtigerum* measure between 0.25 and 0.6 mm long and are designated as villous.

A number of populations of *E. denticulatum* from southern Peru and western Bolivia contain plants that were described by Samuelsson (1923) as *E. hirtum*. These are characterized by long erect or spreading hairs, 0.2–0.4 mm long, which are here termed hirsute. Long hairs of this type intergrade continuously with the slightly shorter strigillose pubescence mentioned earlier, both in length of the hairs and in the degree to which they are appressed.

4. Appressed, blunt-tipped. These are generally small, 0.05–0.1 mm, blunt-tipped hairs that are tightly appressed to both surfaces of the leaf blade. They have been found in only *E. denticulatum* and *E. pedicellare*. The distinction between these hairs and the glandular ones discussed earlier is very fine. The appressed hairs are smaller but merge imperceptibly with the glandular ones in the region of the petiole and lower leaf blade. In living plants, the appressed hairs never produce an exudate. Older leaves are often glabrate, so the appressed hairs may be found only on the younger leaves. In plants of *E. denticulatum* that are hirsute, the hairs on the leaves may also be erect, and are perhaps under the same type of genetic control.

Leaves. The basic leaf type found in South American species is lanceolate, thin, and acute at the apex. In a few instances, however, species deviate from this shape sufficiently for the leaf outline to be a useful taxonomic character. Ovate, thick leaves are typical in *E. australe*, and elliptic to orbicular blades are found in *E. conjungens*.

The type and size of teeth on the leaf margins can also be helpful. The majority of species have few, denticulate teeth. In contrast, the margins of leaves in *E. ciliatum* are usually serrulate with numerous teeth. *Epilobium pedicellare* is quite unusual in having leaves with coarsely serrate margins, the teeth of uneven sizes. The few, narrow, sharply pointed, forward-directed teeth in *E. hirtigerum* are also diagnostic. These last two species are also distinctive in their mostly alternate leaves. Other species normally have opposite leaves, or leaves that are alternate only in the inflorescence.

Inflorescences. Inflorescences in *Epilobium* are only partially useful as a diagnostic feature. They may vary from simple to paniculate and densely branched. The nature of the inflorescence depends upon the branching pattern exhibited by the individual plant. In general, inflorescences are terminal, erect, and highly variable in the total number of flowers produced during a growing season. Each branch of the inflorescence normally presents only one or a few flowers each day, which only last for that given day. As an example, *E. densifolium* seldom produces more than five or six flowers per stem during an entire season. A single plant, however, may bear many more flowers than this because of its densely branched caespitose habit. Flower production in other species is usually much

more prolific. For example, a large plant of *E. ciliatum* may produce several hundred or more flowers in a single season. The nodding inflorescence and flowers of *E. denticulatum* are very characteristic, although this feature may be lost in preparing specimens or if the plants are collected very late in the growing season. *Epilobium conjungens* exhibits one of the most specialized inflorescence types in *Epilobium*. Instead of producing a discrete, terminal, several-flowered inflorescence, it bears only a few flowers singly along the stem, which continues to grow and root at the tip.

Flowers. Most South American species have flowers with petals of varying shades of pale pink to rose purple. White, or nearly white, petals are found in *E. hirtigerum*, *E. conjungens*, many populations of *E. ciliatum*, and occasionally in *E. denticulatum*. *Epilobium puberulum* is unique in having salmon pink petals. Flower size, color, and morphology alone are generally not sufficient to separate any species but are useful in combination with other characters. The only exception to this is *E. puberulum*, which has a very distinct morphology as well as petal color. At anthesis the petals of *E. puberulum* are imbricate and each one is bent at about 90° a short distance above its insertion on the floral tube. Thus, the four petals produce a flat plane at right angles to the axis of the floral tube, with a small circular opening formed by the bends in the petals. The stigma is positioned in this opening at about the same level as the bend in the petals, with the dehiscent anthers of the four longer stamens pressed between the stigma and the petal bend. The four antipetalous stamens have extremely short filaments, usually less than 0.6 mm long, much shorter than in any other species.

Among the other species, there is considerable variation in petal size, with certain ranges characteristic of a few species, such as *E. densifolium*, which has very large petals, but the magnitude of overlap and the variability of some species precludes the use of flower size by itself as a taxonomic character.

Another unique floral feature is the lavender or bluish staminal filaments found in *E. denticulatum* and *E. pedicellare*. Additional notes on floral features are discussed under floral biology.

Seeds. The morphology of seeds has been considered a useful feature in the taxonomy of *Epilobium* for a very long time (e.g., Haussknecht, 1884; Samuelsen, 1923). Within recent years several surveys of seed surface morphology using scanning electron microscopy have been conducted by Berggren (1974), Raven & Raven (1976), Hoch (1978), and Seavey et al. (1977). The last study is of particular importance because it is a worldwide survey of all the sections and includes species from all the continental areas where *Epilobium* occurs.

Three basic types of seed surfaces are recognized by Seavey et al. (1977). *Papillose*: each cell has a more or less prominent, regular or irregular convex portion in the center of the cell. *Ridged*: this is a specialization of the papillose type in which the papillae are flattened laterally and fused or nearly fused end-to-end in longitudinal rows to form ridges. *Reticulate*: the surface cells show only a regular polygonal reticulum formed by the radial walls, without a papilla.

Nearly all of the species of *Epilobium* in South America have papillose seed surfaces, which is the typical surface morphology for the majority of species in

section *Epilobium* (Seavey et al., 1977). Four species have been illustrated in Seavey et al. (1977): *E. denticulatum* (Figs. 64–66; as *E. hirtum*, Figs. 73–75), *E. australe* (as *E. sp.*, Figs. 70–72), *E. densifolium* (as *E. cf. pauciflorum*, Figs. 61–63), and *E. glaucum* (Figs. 67–69), and a fifth, *E. hirtigerum* in Raven & Raven (1976, Fig. 3b). These examples represent the full range of papillose seeds found in South America.

Epilobium ciliatum is the only species in South America that has nonpapillose seeds. This species produces conspicuously ridged seeds, a type known only in *E. ciliatum* and the relictual western North American *E. oreganum* Greene, both members of the *E. ciliatum* complex (Hoch, 1978). Seeds from South and North American populations are illustrated in Seavey et al. (1977, Figs. 169–174). Foveolate cells are also found on the seeds of *E. ciliatum*, but such seeds do not characterize any distinct taxonomic group. Some populations of *E. ciliatum* from southern Patagonia and Tierra del Fuego may have at least part of the upper seed surface with a reticulate pattern. The area covered by foveolate cells varies in size, but the seeds always have longitudinal ridges along the sides and at the micropylar end. This situation is somewhat analogous to that reported by Hoch (1978) for some populations of *E. ciliatum* subsp. *glandulosum* but has not proceeded to the complete elimination of the ridges.

Seed length is variable, ranging from 0.7 to 2 mm, and is somewhat useful as a diagnostic feature. The majority of species have seeds between 0.8 and 1.4 mm long, with substantial variation within species. *Epilobium puberulum* has consistently small seeds, 0.7–0.9 mm long, and *E. densifolium* has the largest seeds, 1.4–2 mm long. Except for the largest seeds of *E. densifolium*, seed size overlaps too broadly to be used alone to separate taxa.

An additional useful character is the short, often rather broad, pellucid chalazal appendage found in six species, *E. ciliatum*, *E. denticulatum*, *E. pedicellare*, *E. fragile*, *E. puberulum*, and *E. nivale* (cf. Seavey et al., 1977; Hoch, 1978).

CYTOGENETICS AND CROSSING RELATIONSHIPS

Cytogenetics. All of the species of *Epilobium* sect. *Epilobium* that have been examined cytologically have a gametic chromosome number of $n = 18$. Numbers for South American species, some of which are reported here for the first time (Table 1), conform to this pattern, which is based on studies of hundreds of strains from all parts of the world (e.g., Seavey & Raven, 1977a, 1977b, 1977c). Chromosomes in *Epilobium* are uniform in morphology. At meiotic metaphase I they are small (2–4 μm long), heteropycnotic, and exhibit no evident karyotypic markers; they are indistinguishable from one another.

In 1968, Mosquin found evidence for reciprocal translocations while examining chromosomal pairing in experimental hybrids between several species. These initial results have been elaborated on considerably by Seavey (1972), Seavey & Raven (1977a, 1977b, 1977c, 1978), and Hair, Raven, & Seavey (1977), so that the number and distribution pattern of reciprocal translocations in section *Epilobium* is now known in some detail.

Three major species groups, which account for nearly all species in sect. *Epilobium*, have been detected on the basis of reciprocal translocation differ-

TABLE 1. Chromosome numbers in South American species of *Epilobium*. All strains formed 18 bivalents in meiosis. Vouchers are deposited at the Missouri Botanical Garden (MO) unless otherwise indicated. Full localities listed under respective species.

<i>E. australe</i> . Chile, Marticorena et al. 475, 834.
<i>E. barbeyanum</i> . Chile, Solomon 4285, 4296.
<i>E. ciliatum</i> subsp. <i>ciliatum</i> . Argentina, Solomon 4712. Chile, Eyerdam 10296 (NY); Marticorena et al. 852, 970; Moore 412 (LA).
<i>E. denticulatum</i> . Bolivia, Solomon 4938. Ecuador, Berry 2522; Weydahl 153 (S).
<i>E. glaucum</i> . Chile, Marticorena et al. 441, 991.
<i>E. hirtigerum</i> . Argentina, Krapovickas & Cristóbal 14675.
<i>E. nivale</i> . Argentina, Gentili in 1975.
<i>E. obscurum</i> . Chile, F. Schlegel 6882.
<i>E. pedicellare</i> . Bolivia, Solomon 5147.
<i>E. puberulum</i> . Chile, Marticorena et al. 1015; Moore 296 (LA).

ences. The chromosomal arrangements that characterize each group have been given the arbitrary designations of AA, BB, and CC (Seavey, 1972; Raven, 1972). Hybrids within chromosomal groups produce 18 pairs of chromosomes at meiotic metaphase I, but those between groups produce various combinations of pairs and rings and/or chains.

The BB arrangement is considered to be the ancestral condition in sect. *Epilobium* for the following reasons. First, one of the two most primitive species in section *Epilobium*, *E. obcordatum* A. Gray from western North America (Raven, 1976), has this arrangement. Second, the other two arrangements, AA and CC, each differ from the BB by a single reciprocal translocation. AA and CC differ from each other by two overlapping reciprocal translocations. Thus, hybrids between plants with the AA and CC arrangements have 15 pairs and a ring or chain of 6 chromosomes at meiotic metaphase I, while hybrids between plants with the AA or CC arrangements and those with the BB arrangement produce 16 pairs and a ring or chain of 4. The simplest hypothesis for the derivation of these chromosomal groups is that the AA and CC arrangements were each derived independently from the BB arrangement. Third, the BB chromosome arrangement characterizes the largest number of species in sect. *Epilobium* and is the most widespread of the three. It is the common arrangement in Eurasia and Africa and the only one found in Australasia. A number of South American species have this arrangement, and it distinguishes a large group of species in North America.

The AA arrangement is primarily restricted to the New World, where it is known from the *E. ciliatum* complex, consisting of five species centered in western North America, several species in South America, and three apparently unrelated species in Europe, *E. alpestre* (Jacq.) Krock., *E. alsinifolium* Vill., and *E. atlanticum* Litard. & Maire, the latter also found in the Atlas Mountains of Morocco.

The third arrangement, CC, is found in a series of closely related, circum-boreal species, including *E. hornemannii* Reichenb., *E. anagallidifolium* Lam., and *E. clavatum* Trel., among others. Also found to have the CC arrangement is the distinctive western North American species *E. luteum* Pursh, which has four-lobed stigmas and cream-colored flowers.

Besides these three arrangements, two additional unique ones have been dis-

TABLE 2. Strains of *Epilobium* used in artificial hybridization experiments. Vouchers deposited at MO; full collection information given under respective species. Acronyms and strain letters are those used in Tables 3 and 4, and Figures 1 and 2. If the name given in Seavey and Raven (1977c) differs from the nomenclature used here, that name has been placed in parentheses after the corresponding strain.

<i>E. australe</i> . (AUST)
(a) Argentina, Moore 1686 (<i>E. sp.</i>).
(b) Chile, Marticorena et al. 834.
(c) Argentina, Rubulis in 1976.
<i>E. barbeyanum</i> . (BARB)
Chile, Solomon 4296.
<i>E. ciliatum</i> subsp. <i>ciliatum</i> . (CIL)
Chile, Zöllner 7868 (<i>E. chilense</i> Hausskn.).
<i>E. ciliatum</i> Raf. subsp. <i>watsonii</i> (Barbey) Hoch & Raven. (WAT)
U.S.A., California, Sharp in 1967 (<i>E. watsonii</i> Barbey).
<i>E. densifolium</i> . (DENS)
(a) Chile, Zöllner 6245 (<i>E. cf. pauciflorum</i> F. Phil.).
(b) Argentina, Diem 3600.
<i>E. denticulatum</i> . (DENT)
(a) Argentina, Hunziker & Ariza 20424.
(b) Perú, Conrad 2715.
(c) Perú, Averett 1004 (<i>E. hirtum</i> Samuelsson).
<i>E. glaucum</i> . (GLAU)
(a) Chile, Marticorena et al. 7.
(b) Chile, Marticorena et al. 951.
<i>E. hirtigerum</i> . (HIRTIG)
(a) New Zealand, Raven 25148.
(b) Argentina, Krapovickas & Cristobal 14675.
(c) Argentina, Troncoso et al. 2462.
(d) Argentina, Solomon 4131.
<i>E. nivale</i> . (NIV)
Argentina, Gentili in 1975.
<i>E. obscurum</i> . (OBS)
(a) Spain, Raven 26069.
(b) Chile, Ramirez in 1975.
<i>E. puberulum</i> . (PUBER)
Chile, Marticorena et al. 1015.

covered. The first, termed DD, is found in *Epilobium duriaei* Gay ex Godron from Europe (Seavey & Raven, 1977a); the other, termed EE, is found in *E. platystigmatosum* from eastern Asia (Seavey & Raven, 1978). Each of these arrangements differs from the BB by a single reciprocal translocation, and each is different from the AA and CC arrangements. Like the latter two arrangements, DD and EE were probably independently derived from the BB type.

The chromosomal arrangements and some of the crossing relationships within the South American species have now been elucidated. Most of the strains used by Seavey & Raven (1977c), plus a number of additional ones, including several previously uncultivated species, were grown and experimentally hybridized. The hybrid progeny were then examined for chromosomal arrangement and pollen stainability. The strains used in the crossing experiments are given in Table 2, and the results from the hybrids are shown in Tables 3 and 4.

As in previous studies of chromosomal arrangements in *Epilobium*, beginning with those of Seavey & Raven (1977a) and continuing to the present, all of the strains were standardized by crossing them with a single strain of *E. ciliatum*

TABLE 3. Experimental hybrids between species of *Epilobium*. Acronyms and lettered strains refer to Table 2. Female parents are listed first, in alphabetical order, followed by the male parent. Data for voucher numbers below M600 are taken from Seavey and Raven (1977c). All vouchers are deposited at MO; full collection information given under respective species.

Cross	Chromosomal Configuration		Pollen Stainability %	Greenhouse Voucher
AUSTa × CIL	16 _{II} + ch4	BB × AA	32	M465
DENTb	16 _{II} + r4	BB × AA	45	M435
DENTc	16 _{II} + ch4	BB × AA	39	M467
GLAUa	18 _{II}	BB × BB	65	M437
WAT	16 _{II} + r4	BB × AA	26	M469
AUSTb × DENTc		BB × AA	8	M1542
AUSTc × DENTc		BB × AA	11	M1557
PUBER	16 _{II} + r4	BB × AA	38	M1562
BARB × DENTc	16 _{II} + r4	BB × AA	12	M1948
GLAUa	18 _{II}	BB × BB	69	M1953
CIL × AUSTa	16 _{II} + r4	AA × BB	27	M466
BARB	16 _{II} + r4	AA × BB	33	M1954
DENTa	18 _{II}	AA × AA	37	M455
DENTb	18 _{II}	AA × AA	51	M1540
DENTc	18 _{II}	AA × AA	56	M1538
GLAUa	16 _{II} + ch4	AA × BB	23	M443
WAT	18 _{II}	AA × AA	86	M1539
DENSa × GLAUa	18 _{II}	BB × BB	88	M441
OBsa	18 _{II}	BB × BB	0	M575
DENSb × GLAUa	18 _{II}	BB × BB	92	M1552
DENTb × AUSTa	16 _{II} + r4	AA × BB	45	M436
CIL	18 _{II}	AA × AA	47	M456
DENSa	16 _{II} + r4	AA × BB	15	M452
GLAUa	16 _{II} + ch4	AA × BB	41	M439
OBsa	16 _{II} + r4	AA × BB	33	M459
WAT	18 _{II}	AA × AA	24	M457
DENTc × AUSTa	16 _{II} + ch4	AA × BB	34	M468
AUSTb		AA × BB	7	M1541
AUSTc	16 _{II} + r4	AA × BB	25	M1556
CIL	18 _{II}	AA × AA	64, 61	M1537, M1964
BARB		AA × BB	21	M1949
DENSb	16 _{II} + r4	AA × BB	27	M1550
GLAUa	16 _{II} + ch4	AA × BB	29	M444
OBsb		AA × BB	31, 18	M1561, M1967
GLAUa × AUSTb	18 _{II}	BB × BB	84	M1543
AUSTc		BB × BB	97	M1558
CIL	16 _{II} + r4	BB × AA	22	M442
DENSb		BB × BB	87	M1551
DENTb	16 _{II} + r4	BB × AA	46	M440
DENTc	16 _{II} + r4	BB × AA	24	M445
PUBER		BB × AA	44	M1546
GLAUb × AUSTc	18 _{II}	BB × BB	83, 68	M1559, M1966
NIV × DENTc	16 _{II} + r4	BB × AA	13	M1554
GLAUa	18 _{II}	BB × BB	23, 12	M1555, M1965
OBsa × DENSa	18 _{II}	BB × BB	0	M576
DENTb	16 _{II} + ch4	BB × AA	36	M460
GLAUa	18 _{II}	BB × BB	21	M448
PUBER × BARB	16 _{II} + r4	AA × BB	56	M1952
GLAUa	16 _{II} + r4	AA × BB	47	M1547
WAT × AUSTa	16 _{II} + r4	AA × BB	24	M470
DENTb	18 _{II}	AA × AA	37	M458

TABLE 4. Experimental hybrids involving *Epilobium hirtigerum*. Acronyms and lettered strains refer to Table 2. Female parents are listed first, in alphabetical order, followed by the male parent. Data for voucher numbers below M600 are taken from Seavey and Raven (1977c). All vouchers are deposited at MO; full collection information given under respective species.

Cross	Chromosomal Configuration		Pollen Stainability %	Greenhouse Voucher
DENTa × HIRTIGb	14 _{II} + r4 + ch4	AA × B ₁ B ₁	9	M462
GLAUa × HIRTIGb	16 _{II} + r4	BB × B ₁ B ₁	9	M451
HIRTIGa × HIRTIGb	16 _{II} + r4	BB × B ₁ B ₁		
HIRTIGb × DENTa	14 _{II} + 2 r4	B ₁ B ₁ × AA	14	M463
GLAUa	16 _{II} + r4	B ₁ B ₁ × BB	7	M450
HIRTIGc	16 _{II} + r4	B ₁ B ₁ × BB	38	M1958
HIRTIGd	16 _{II} + r4	B ₁ B ₁ × BB	52	M1955
HIRTIGc × OBSa	18 _{II}	BB × BB	64	M1959
HIRTIGd × OBSa	18 _{II}	BB × BB	60	M1960
PUBER × HIRTIGc		AA × BB	1	M1961

subsp. *watsonii* (WAT; AA), *E. obscurum* (OBSa; BB), or with another strain that had previously been standardized to the first two.

Only the AA and BB chromosomal arrangements are present in South America. Their distribution among the species is summarized in Table 5. The rationale for the suspected arrangement of the three unknown species is discussed in the section on biogeographical relationships.

Epilobium puberulum is presented as having the AA genome. When this species was crossed with *E. glaucum*, a known BB, the resulting hybrids produced 16 pairs and a ring of four chromosomes at meiotic metaphase I. There is no evidence to suggest that *E. puberulum* has an unusual chromosome arrangement, so it will probably be found to have the AA arrangement. The definitive crosses to known AAs have been made but not yet analyzed.

Epilobium hirtigerum initially presented a perplexing chromosomal situation. The original strain that was tested (HIRTIGb) was found to differ from the BB arrangement by one reciprocal translocation and from the AA by two. The question was posed as to whether this unusual arrangement characterized all populations of *E. hirtigerum* in South America (Seavey & Raven, 1977c). Two additional populations, one (HIRTIGd) from the same general area, and a second from elsewhere in the range (HIRTIGc), were tested against the original strain and a known BB. The results of these crosses are given in Table 4. It now appears likely that the BB arrangement is the normal one for *E. hirtigerum* in South America, as it is in Australasia, and that the original strain tested is atypical.

Plants with anomalous chromosomal arrangements, such as that illustrated by *E. hirtigerum*, are now known in four species. In *E. microphyllum* A. Rich. and *E. palustre* L., single individuals have been found that differed from the BB arrangement by one reciprocal translocation. Other plants of these species from the same or nearby populations, however, had the BB arrangement (Raven, 1972; Seavey & Raven, 1977a). In a similar fashion, a single individual of *E. glaberrimum* Barbey had an arrangement that differed from AA by one reciprocal translocation, but plants from the same and a number of other populations were all

TABLE 5. Distribution of chromosomal arrangements in native South American species of *Epilobium*. See text for further explanation of species marked with asterisk (*).

Species	Arrangement
<i>E. denticulatum</i>	AA
<i>E. puberulum</i>	AA*
<i>E. ciliatum</i>	AA
<i>E. nivale</i>	BB
<i>E. barbeyanum</i>	BB
<i>E. densifolium</i>	BB
<i>E. australe</i>	BB
<i>E. glaucum</i>	BB
<i>E. hirtigerum</i>	BB*
<i>E. pedicellare</i>	Not known, probably AA
<i>E. fragile</i>	Not known, probably AA
<i>E. conjungens</i>	Not known, probably BB

AA (Seavey & Raven, 1977a). It seems clear that these chromosomally differentiated plants probably arose spontaneously within populations. Events of this type provide an example of how the major chromosomal lines might have arisen and how differentiation between species could have proceeded.

Crossing relationships. It has been well established that there are essentially no barriers to the production of viable seed between members of *Epilobium* sect. *Epilobium*, even among geographically and morphologically separated species or between chromosomal groups (e.g., Brockie, 1970; Seavey & Raven, 1977a), although various types of genetic or cytoplasmic incompatibilities may seriously disrupt development or fertility after germination (Thakur, 1965). The failure to set seed in interspecific crosses may occur due to poor pollen tube growth, or failure of fertilization, but these are generally not important factors (Raven & Raven, 1976). The results of this study support this broad conclusion. Seed set may be reduced in artificial crosses, but this is often due to technical difficulties, such as damage to small flowers when they are emasculated, transfer of an inadequate quantity of pollen, or use of pollen from a short-styled species to cross with a long-styled one. In all cases, at least some seed was produced in interspecific crosses.

The hybrids that were made with the South American species, with few exceptions, showed no developmental abnormalities or reciprocal differences such as those that have been reported by Thakur (1965), Michaelis (1954, 1965), and Raven & Raven (1976). Hybrids between *E. obscurum*, a European species, and *E. densifolium*, *E. glaucum*, and *E. australe* were all initially dwarf. Only one plant of the hybrid combination *E. obscurum* × *E. glaucum* eventually flowered vigorously. The other combinations either died or flowered only sporadically (Seavey & Raven, 1977c). Similarly, hybrids between *E. denticulatum* and *E. obscurum* were also initially dwarf, and only two individuals eventually produced normal branches and flowered. These hybrids, which involved both the AA and BB chromosomal groups (Table 5), would strongly suggest some type of genetic or cytoplasmic incompatibility specifically with *E. obscurum*, although its precise nature is not known. The hybrid between *E. nivale* and *E. glaucum* may also

have been disturbed developmentally. Although the plants were vigorous vegetatively, they produced very few flowers. Alternatively, this could be the result of the relatively low number of flowers that *E. nivale* normally produces under greenhouse conditions.

In the absence of obvious developmental barriers to hybridization, one must utilize other data to assess the degree of relationship between species. Besides the chromosomal arrangements that divide the South American species into two groups, hybrid fertility, as indexed by the percentage of stainable pollen (Table 6), can also be used as a measure of relationship. This data must be used cautiously, however, because pollen stainability can vary considerably from plant to plant and even between flowers on the same plant, and it is often greatly affected by the age of the plant and the cultural conditions under which the plant has been grown.

The pollen fertility of most non-hybrid plants used in the experimental hybridizations was greater than 85%, with two exceptions, *Epilobium denticulatum* (DENTc), which had 75%, and *E. barbeyanum* (BARB), which had 54%. Even crosses made between strains of the same species from widely separated geographical areas had high fertility (e.g., *E. denticulatum*: Averett 1004, Peru × Billings 161, Venezuela, 94%; *E. ciliatum* subsp. *ciliatum*, Zöllner 7868, Chile × *E. ciliatum* subsp. *watsonii*, Sharp in 1967, California, 86%).

The much reduced pollen fertility seen in Table 6 between species with different chromosomal arrangements is due primarily to the high frequency of adjacent disjunction of the chromosomes involved in the ring of four during meiosis. The consequent duplications and deletions resulted in a substantial number of aborted gametes (Seavey, 1977). Hybrids between species with the same chromosomal arrangement that show reduced fertility must have other factors involved.

Epilobium ciliatum and *E. denticulatum*, both with the AA arrangement, have differentiated genetically and produce hybrids with substantially reduced fertility. Within the group of species with the BB arrangement, *E. glaucum* when crossed with *E. australe* or *E. densifolium* produces hybrids with variable, but sometimes very high, fertility, up to 97% and 92% respectively (Table 6). These values are similar to those reported for hybrids between many closely related species in Australasia (Raven & Raven, 1976). This suggests that these three species are fairly closely related to one another, although they are morphologically distinct. The relationship of *E. barbeyanum* to these species is still obscure. *Epilobium nivale*, on the other hand, is quite strongly differentiated from *E. glaucum*, either genetically or cytoplasmically, as indicated by the very low hybrid pollen stainability and the disturbed development mentioned earlier. Its relationship with the other species remains unknown.

BIOGEOGRAPHICAL RELATIONSHIPS

The morphological and cytological evidence presented previously suggests that there have been a minimum of five pre-European introductions of *Epilobium* into South America with subsequent diversification in some of these lines. The probable source of progenitors for each group and the relationships of the cur-

TABLE 6. Percent of stainable pollen in experimental hybrids of *Epilobium*. Acronyms refer to Table 3.

	♂/♀	AA				BB				STANDARDS		
		DENT	PUBER	CIL	NIV	BARB	DENS	AUST	GLAU	HIRTIG	OBS	WAT
AA	DENT	.	.	47, 61, 65	.	21	15, 27	7, 25, 34, 45	29, 41	.	18, 31 33	24
	PUBER	56	.	.	47	1	.	.
	CIL	37, 51, 56	.	.	.	33	.	27	23	.	.	86
BB	NIV	13	12, 23	.	.	.
	BARB	12	69	.	.	.
	DENS	88, 92	.	0	.
	AUST	8, 11, 39, 45	39	32, 34	65, 76	.	.	26
	GLAU	24, 46	44	22	.	.	87	68, 83, 84, 97
STANDARDS	HIRTIG	64, 60	.
	OBS	36	0	.	21	.	.	.
	WAT	37	24

TABLE 7. Distribution and probable sources of progenitors for related groups of native species of *Epilobium* in South America. AA and BB refer to chromosomal arrangements; see text for further discussion.

Group/Species	Distribution	Source of Progenitor
Group I (AA)		North America
<i>E. denticulatum</i>	Andes, Venezuela to northern Argentina and Chile; Costa Rica	
<i>E. fragile</i>	Altiplano of Peru and Bolivia	
<i>E. pedicellare</i>	Altiplano of Peru and Bolivia	
<i>E. puberulum</i>	Central Chile	
Group II (AA)		North America
<i>E. ciliatum</i>	Southern Andes of Chile and Argentina, Falkland Islands; widespread in North America	
Group III (BB)		Australasia
<i>E. australe</i>		
<i>E. barbeyanum</i>	Southern Andes of Chile and Argentina	
<i>E. densifolium</i>		
<i>E. glaucum</i>		
<i>E. nivale</i>		
Group IV (BB)		Australasia
<i>E. hirtigerum</i>	Eastern Argentina, Uruguay and southern Brazil; widespread in Australasia	
Group V (BB)		Australasia
<i>E. conjungens</i>	Tierra del Fuego and adjacent islands	

rently recognized species are summarized in Table 7 and discussed in detail below.

The two groups with the AA chromosomal arrangement almost certainly have ancestral affinities with North America. These are the only species with the AA arrangement in the Southern Hemisphere. The other species with this arrangement are found primarily in North America, with only three isolated species in western Europe.

Epilobium denticulatum is the most widespread and variable species of the first group in Table 7, and highly characteristic of the páramos and puna throughout the northern and central Andes. Although *E. pedicellare* and *E. fragile* are unknown chromosomally, they appear to be closely allied to *E. denticulatum* on morphological grounds, and will probably be found to have the AA chromosomal arrangement. *Epilobium pedicellare* shares with *E. denticulatum* the feature of appressed, blunt-tipped hairs on the leaf surfaces, a similar habit, and completely overlapping geographical ranges. The relationships of *E. fragile* are somewhat more problematical because of its reduced stature and restriction to extremely high elevations, but it is probably closely related to and may be directly derived from *E. denticulatum*. The geographical range of *E. fragile* is also completely contained in that of *E. denticulatum*, and some small specimens of *E. denticulatum* approach *E. fragile* in overall morphology. Certainly this might be the result of convergence, but no alternative placement for *E. fragile* is apparent. These three species are the only ones found in the northern and central Andes; all of

the others are restricted to areas mostly south of 30°S latitude. *Epilobium puberulum*, although isolated geographically in central Chile from the species discussed above, is morphologically similar to some populations of *E. denticulatum* and has often been confused with that species.

The precise relationships between these four species is not clear, and none of them resemble any extant North American species, but North America is the only reasonable source for progenitors, which probably arrived in South America by long-distance dispersal. The ancestor of these species was probably an early offshoot of the AA chromosomal line that gave rise to the members of the *E. ciliatum* complex in North America (Hoch, 1978).

The second AA chromosomal group consists only of *Epilobium ciliatum* subsp. *ciliatum*. The South American populations, which are found in areas south of 30°S, have gone under various names, most often *E. chilense*, *E. valdiviense*, or *E. magellanicum*. Only recently has the question been raised as to whether populations from South America were closely related to ones from North America (Seavey et al., 1977; Seavey & Raven, 1977c), although some South American plants had been identified as North American species and vice versa many years ago (Haussknecht, 1879, 1884).

In 1977, Seavey et al. discovered that the seed surface morphology of plants identified as *Epilobium chilense* were identical with those found in *E. ciliatum* in North America. As was discussed earlier, this seed type is restricted to two species in North America. In addition, these South American plants produced turions or leafy rosettes, overwintering structures that are unique in South America but are common in a number of species in North America. An analysis of the *E. ciliatum* complex in North America by Hoch (1978) provided additional morphological features as a basis for comparison. In this study he recognized five species, including *E. glaberrimum* Barbey with two subspecies and *E. ciliatum* with three subspecies. A careful comparison of plants from many widely separated South American populations with others from North America indicated that there were few differences between them and that all the South American populations could easily be accommodated in *E. ciliatum* subsp. *ciliatum* as circumscribed by Hoch. In fact, the variability seen in South America is only a part of that exhibited by this subspecies in North America, where it is extremely diverse and widespread. *Epilobium ciliatum* in South America has been derived from North America and may have originated from a single introduction.

There is an unlikely possibility that *Epilobium ciliatum* arrived in South America as an unintentional introduction by man. Beginning in the 1760s, with the founding of a number of missions in Alta California, increased commerce began between the western coast of North America and Peru and Chile. Prior to this time, only rare and casual visits had been made to North American areas where *E. ciliatum* occurs. Thus, the most likely time of introduction would have been after this date. The first South American collections of *E. ciliatum* were made about 1793 in central Chile, and by 1833 in Tierra del Fuego, a period of only 40 years. Considering the extensive variation and presence of *E. ciliatum* in many areas that were remote from human habitation over a geographic distance of 2,700 km in South America, it seems unlikely that *E. ciliatum* has been introduced within the past 200 to 300 years. Rather, its occurrence in South America is

probably the result of a pre-European long distance dispersal event (cf. Raven, 1963).

The species with the BB chromosomal arrangement, however, probably have their affinities with Australasian species. They have been divided on the basis of morphology into three groups, one with five species, the other two with one each, representing three independent introductions (Table 7).

Epilobium australe, *E. barbeyanum*, *E. densifolium*, and *E. glaucum* are fairly closely related, with *E. nivale* being somewhat anomalous, but also probably allied. These species are morphologically unlike any North American species with the BB chromosomal arrangement, but they also show no obvious affinities with any extant species in Australasia. The habit, simple leafy shoots as perennating structures, and the rather broadly obovoid seeds (cf. Raven & Raven, 1976) suggest an Australasian relationship.

Epilobium hirtigerum is conspecific with a widespread species of Australia and New Zealand. For many years the South American populations were called *E. brasiliense*. However, during the intensive study that led to their monograph of *Epilobium* in Australasia, Raven & Raven (1976) discovered that the South American plants were indistinguishable from those found in many populations in Australasia, especially New Zealand. The examination of a large sample of specimens from South America for the present study confirms this conclusion. Philibert Commerson made collections of this species in Uruguay two years prior to the first known European landings in eastern Australia or New Zealand by Captain James Cook in 1769. Unless some unknown, fortuitous historical event aided introduction of this species, it seems highly probable that *E. hirtigerum* arrived in South America by long-distance dispersal. It also seems likely that the present populations were derived from a single introduction from Australasia.

The third group contains only *Epilobium conjungens*. This species has what can be considered the most unusual morphology of any South American species. The stems are prostrate, growing and rooting beyond the flowers, producing small mats, with the flowers scattered singly, often widely, along the stem, and with consistently opposite leaves. This combination of features is shared with 13 species restricted to Australasia and no others. In describing *E. conjungens*, Skottsberg (1906) drew attention to its apparent close relationship to the creeping species of Australasia and placed it nearest to *E. nummulariifolium* A. Cunn. and *E. brunescens* (Cockayne) Raven & Engeln (as *E. pedunculare* A. Cunn.), based on Haussknecht's *Monographie* (1884). He considered it "ein weiteres Bindeglied," a wide (distant) connecting link between the floras of Tierra del Fuego, where *E. conjungens* is endemic, and New Zealand. The epithet "conjungens," chosen by Skottsberg, reflects this relationship, meaning connected or united, and referring to its floristic affinities.

More recently, the distinctive habit of *Epilobium conjungens* was interpreted to be the result of convergent evolution, since it was believed that *E. conjungens* had a few flowered, terminal inflorescence (Raven & Raven, 1976). An examination of material unavailable to them, however, shows clearly that *E. conjungens* possesses all the features that are unique to the creeping Australasian species. In addition, the flowers of *E. conjungens* are white as they are in all other creeping species. It seems certain that *E. conjungens* was derived from an Australasian

progenitor. Although the chromosomal arrangement of *E. conjungens* is not known, the presence of only the BB type in Australasia suggests that *E. conjungens* will be found to have that arrangement also.

Ancestors of these three groups probably arrived by long-distance dispersal via the prevailing westerlies. These winds blow continuously, between 30° and 60°S latitude, and are four times as strong as their Northern Hemisphere counterparts (Lamb, 1959). They have undoubtedly played an important role in the dispersal of organisms between southern land masses (Raven, 1973a). *Epilobium* seeds are highly dispersable by wind. Each seed has a coma of long silky hairs at the chalazal end. Once the capsule has dehisced, the seeds can be moved many meters by even light breezes.

A striking representation of the capacity of the Southern Hemisphere westerly winds to affect movement between Australasia and southern South America is illustrated by a recent balloon experiment (Mason, 1971). A radio controlled balloon was released from Christchurch, New Zealand, held at about 12,000 m, and followed by satellite. During the 102 days of tracking, it made eight circuits of the globe, and repeatedly crossed south Australia, New Zealand, southern South America, and southern Africa. On most circuits it required only four to six days to traverse the distance between New Zealand and South America. Of special interest in connection with this pattern of dispersal is the presence of 13 species of *Epilobium* in the Chatham Islands, 800 km east of New Zealand. Equally suggestive of an initial origin in Australasia for the three groups of species with the BB chromosomal arrangement now found in South America is that all of them are restricted to areas south of 30°S latitude, precisely in the path of the prevailing winds. With their high fecundity and persistent autogamy, the introduction of a single *Epilobium* seed in a suitable habitat would provide the basis for a founding population.

The foregoing discussion clearly shows the diverse origins of *Epilobium* in South America and provides examples of two major types of temperate disjuncts found in the New World, amphitropical and circumaustral (Moore, 1972; Raven, 1963, 1973b), both at the individual species level and at higher species groupings. The data available for *Epilobium* reinforces the conclusions of the papers just cited, that most disjuncts in common between North and South America have been derived by dispersal from north to south, and those between Australasia and South America from west to east.

EVOLUTIONARY HISTORY

The time of arrival and the impact of geological events on the various groups of *Epilobium* in South America is important to an understanding of their evolutionary history. In the absence of any fossil data on *Epilobium* in South America, except in a few apparently recent (late Pleistocene) but poorly dated pollen samples from Patagonia and Tierra del Fuego (Auer, 1958), the evidence for the time of appearance of *Epilobium* in South America is dependent on information about the availability of suitable habitats and on the presence of *Epilobium* in the presumed source areas.

As was discussed earlier, the genus *Epilobium*, based on its current distribution, possibly evolved in western North America and spread from there throughout the Northern Hemisphere, entering the three Southern Hemisphere continents only secondarily. In Australasia, *Epilobium* apparently did not arrive from Asia until the late Pliocene (Raven, 1973a; Raven & Raven, 1976). Prior to this time, from the Cretaceous to the mid-Miocene, Australasia was much further south than it is at the present and was separated initially by a gap of at least 3,000 km from points in southeast Asia (Raven, 1979b). During this period, Australasia was dominated by temperate forests (Raven, 1973a), while southern Asia was tropical, with low relief (Raven, 1979b), and hence, an area unlikely to have had *Epilobium* at that time. It was only during the late Pliocene, after Australasia had moved sufficiently far northward to encounter the Asian Plate, that mountains with cool-temperate climates were formed in Malaysia, Sumatra, Luzon, and New Guinea that could serve as intermediate points for the long-distance migration of temperate Asian species into Australasia. The earliest records of *Epilobium* in New Zealand are from the late Pliocene (Raven & Raven, 1976). Thus, Australasia could not have served as a source area for *Epilobium* in South America until at least the late Pliocene, and probably later.

North and South America were widely separated until the Eocene, at which time South America was more or less equidistant from Africa and North America. From that point on, they moved closer to one another and gradually underwent orogenies that eventually resulted in a land connection about 3.1 million years ago (Keigwin, 1978; Marshall et al., 1979). Suitable temperate habitats for *Epilobium*, however, did not occur in South America throughout that time, except perhaps in the far South where *Nothofagus* forests similar to those in Australasia existed (Simpson, 1973; Vuilleumier, 1969).

A review of palynological and geological studies suggests that the Andes are a very recently evolved mountain range that did not attain high elevations until the late Pliocene or even the early Pleistocene (Flenley, 1979; Hammen, 1974, 1979; Simpson, 1975, 1979). The present-day Andes are composed of a rather large number of structural-tectonic units that have undergone separate orogenies involving uplift, folding, faulting, and vulcanism, but resulting in a more or less concurrent elevation of the entire range.

At the end of the Cretaceous most of the land that now forms the Andes had been elevated above sea level and gradual uplifting continued until the Miocene. During this time, elevations in excess of 1,000 m were probably infrequent, at least in the north (Hammen, 1979). Throughout most of this period the Andean region was covered with tropical forests that extended much farther south than at present and merged gradually with subtropical and temperate forest elements in the far south (Cei, 1979).

Beginning in the Miocene and continuing into the Pliocene increased vulcanism and crustal movements uplifted the mountains even more, but it is doubtful if there were significant areas of elevation over 2,000 m (Simpson, 1979).

During this same period, the initial phases of climatic deterioration in southern South America began, which ultimately culminated in the glacial events of the Pleistocene. The major trend was toward a cooler, drier climate, with increasing

rain shadow effects from the rising Andes, which resulted in the breakup of Patagonian forest lands and the migration of more mesic tropical and subtropical elements northward (Báez & Scillato, 1979).

The middle and late Pliocene saw a major increase in orogenic activity that continued into the Pleistocene and resulted in an average uplift of 1,000 to 3,000 m throughout the Andes. Thus, all of the floristic elements that are currently found at high elevations must have been derived during the past two to five million years, either by migration from other temperate areas or by vertical evolution from pre-existing lowland tropical elements (cf. Cleef, 1979).

The first indication of open páramo-like habitats is found in the northern Andes in upper Pliocene formations and consists of a high representation of Gramineae, Compositae, and *Hypericum* (Hammen, 1979). All the species of *Epilobium* of apparently North American extraction (AA), except *E. ciliatum* and *E. puberulum*, occur in the páramo and puna north of central Chile and Argentina. It is unlikely that the North American progenitor of these species could have arrived and become established prior to the late Pliocene, and it may have appeared even later.

Species such as *E. ciliatum* and *E. hirtigerum* probably arrived during or after the last glaciation. The ancestor of *E. conjungens* almost certainly arrived after the last glacial advance, since Tierra del Fuego and adjacent islands, where it is endemic, were completely ice-covered at that time (Vuilleumier, 1971).

Climatic deterioration in the late Tertiary finally resulted in the drastic fluctuations between glacial and interglacial climates that characterized the Pleistocene. Tropical regions were significantly affected by alternating climates just as were more temperate areas.

In the tropical Andes, there is evidence for one to four glaciations that, during the last glacial advance, resulted in the lowering of tree line from 1,200–1,500 m below its present level, and a reduction of mean temperature by 6–7°C, at least in the Andes of Colombia (Hammen, 1974). Glacial periods were colder and drier than interglacials, resulting in the downward movement of vegetation zones, generally with an increase in their areal extent, and expansion of some xeric vegetation types at the expense of moist or wet tropical ones, especially in the lowlands (Haffer, 1979). The impact of actual glacial ice during these periods was not as great in the tropics as the heavy glaciation in more temperate latitudes; although substantial glaciation took place in the cordilleras of Peru and Bolivia and on other high mountains elsewhere (Vuilleumier, 1971). During interglacials, the climate was warmer and probably wetter, resulting in an upward movement of vegetational zones, contraction of páramo vegetation and an expansion of more mesic forest types. For páramo and dry lowland floras, the interglacials were a time of isolation and differentiation, and vice versa during glacials.

In temperate South America, the impact of glacial events was in many ways much more severe than in the tropics. There is abundant evidence for four glaciations that covered large areas of the southern Andes with glacial ice. Between 30°S and 44°S there were extensive montane glaciers extending to progressively lower elevations. Some of these produced major ice barriers in a number of river valleys in central Chile (Simpson, 1979). From about 44°S latitude the entire Andes chain was covered with glacial ice to sea level on the western slope and

to the base of the mountains on the east. The area covered by ice included all of Tierra del Fuego and the southern tip of Patagonia (Vuilleumier, 1971). Glacial advances effectively lowered vegetation zones in temperate South America, which allowed alpine and other high elevation vegetation to cover more extensive, continuous areas and produce regions of secondary contact between formerly isolated populations. At the same time, it caused contraction and shifting of *Nothofagus* forest regions northward (Simpson, 1973). During interglacials these same alpine vegetation types were isolated in upper montane areas where they could undergo independent differentiation.

The effects of Pleistocene climatic fluctuations on speciation patterns in *Epilobium* are not at all clear, and may have had relatively little impact, unlike patterns found in other Andean groups that have apparently diversified greatly under alternate contraction and expansion of ranges (e.g., *Perezia multiflora* complex, Simpson, 1973; *Arracacia*, *Lleracia*, Simpson, 1975). Of the tropical species, only *E. denticulatum* shows extensive morphological diversity through its large range in the páramo and puna. Interestingly enough, *E. denticulatum* achieves its greatest variability in the altiplano and cordilleras of Peru and Bolivia, with diminishing diversity both north and south of there. This area is the part of the range of *E. denticulatum* that was most heavily glaciated during the Pleistocene, so glacial advances and retreats may have influenced the variation patterns now seen. The high dispersability of *Epilobium* seed, however, may exclude glaciers from acting as actual barriers. Alternatively, this great diversity may be due to the large number of habitats at various elevations available for colonization by *E. denticulatum* in this region.

Unlike *Epilobium* in New Zealand, which has undergone an explosive radiation of many closely related species adapted to a diverse array of habitats through hybridization and persistent autogamy, the largest group of closely related species in South America contains only five members (*E. australe*, *E. barbeyanum*, *E. densifolium*, *E. glaucum*, and *E. nivale*). Each of these is very distinctive, with mostly overlapping ranges, and no one of them can be said to have been derived by hybridization between any other two species. These species may have evolved under the isolation-habitat specialization model suggested above, but at the present time interpretation of their inter-relationships remains perplexing and awaits new insight.

Pleistocene glacial advances also affected the current geographical distribution of some of the species. All of the species except three are found almost exclusively south of 30°S. Between the latitudes of 27°S and 31°S there was a band of persistent aridity that crossed the Andes and was an effective barrier during both glacial and interglacial periods (Simpson, 1979). *Epilobium ciliatum*, *E. glaucum*, and *E. barbeyanum* all reach their northern limits at the southern edge of this zone. Only *E. denticulatum* has managed to cross this barrier in a narrow strip along the eastern slope of the Andes, south to about 34°S. In southern South America, the heavy glaciation south of 44°S, eliminated much of the montane vegetation. There are a large number of species that reach their southern limit at about this latitude (Simpson, 1973), including *E. barbeyanum* and *E. densifolium*, which are not known from south of about 42°S.

One of the more peculiar distributions seen in *Epilobium* is that of *E. nivale*.

It too reaches the southern limit of its primary range at about 42°S, but then reappears in the vicinity of Lago Argentino (51°S), indicating a gap in its range of about 800 km. Other species, such as *Isoetes savatieri* Franch. (Donat, 1931), the species pair *Perezia bellidifolia* (Phil.) Reiche and *P. megalantha* Speg. (Simpson, 1973), and *Gunnera tinctoria* (Mol.) Mirbel (Pisano, pers. comm.), have similar distributions, which has led some authors (Auer, 1958; Skottsberg, 1916; Donat, 1931; Simpson, 1973) to suggest that there was a refugial area to the east of the Andes in the far south where these and other species managed to survive during the heaviest glaciations, while they were eliminated in between. It is possible that *E. nivale* does occur in the intervening area because the Patagonian Andes have been little explored botanically, and *E. nivale* inhabits high, relatively inaccessible areas near the snow line.

REPRODUCTIVE BIOLOGY AND HYBRIDIZATION

Breeding system. The majority of the species of *Epilobium* sect. *Epilobium* are autogamous, with only approximately 10% of the 170 species modally outcrossing. All are self-compatible, and, in those that are capable of self-fertilization, a full complement of seed is normally produced.

Epilobium species in South America possess a diversity of breeding systems, from modally outcrossing to cleistogamous, but all of them can produce seed by self-fertilization (see review in Raven, 1979a). Nearly all the species have pale pink to rose purple flowers, including the three introduced species. Only *E. hirtigerum*, *E. denticulatum*, *E. ciliatum*, and *E. conjungens* have petals that are white or vary from white to pink. Flower color appears to be significantly related to the degree of outcrossing, as pointed out by Raven & Raven (1976), since insects are more likely to visit the colored flowers than white ones.

Epilobium densifolium has the largest number of features typical for a modally outcrossing species. The flowers are large (petals up to 1.2 cm long), with the anthers held away from the stigma at anthesis, and usually the stigma partially exerted. Each flower produces a large droplet of nectar. *Epilobium australe*, *E. glaucum*, and *E. barbeyanum* have smaller flowers, but in them also, the anthers are held away from the stigma at anthesis. In these four species, usually after a period of several hours, the longest stamens gradually bend inward and the dehiscent anthers make contact with the receptive stigma. Nonetheless, they are all modally outcrossing.

Epilobium denticulatum has separate or even mixed populations of large- and small-flowered plants. In this species, the large flowers also have the anthers separated from the stigma, at least for a few hours. The balance of the species, including the small-flowered populations of *E. denticulatum*, have flowers that are more or less immediately self-pollinated at anthesis. Functional cleistogamy seems to be the general condition for *E. hirtigerum*, where the anthers may dehisce prior to the opening of the flower bud. Generally, the anthers dehisce at anthesis, although there may be up to a few hours delay. In addition, all species, except *E. hirtigerum* and some plants of *E. ciliatum*, produce at least a small amount of nectar that may be attractive to flower visitors.

Weather conditions have a very strong effect on the extent to which the

flowers of *Epilobium* open at anthesis. All species open their flowers fully on bright sunny days, including *E. hirtigerum*. On cloudy or rainy days, however, most plants open their flowers only partially or not at all, very strongly reducing the chances of cross-pollination or eliminating that possibility completely by being functionally cleistogamous.

Despite the various features that might promote some outcrossing, insect visitation to any of the species appears to be quite rare. In many hours of observation, at all times of the day and under various weather conditions, only two insect visitors were observed. Several unidentified medium-sized syrphid flies were seen visiting flowers of *Epilobium barbeyanum* in a large streamside bog near Lagunillas, Cordillera Prov. (Santiago), Chile; and a single visit by a small, unidentified bee to several plants of *E. denticulatum* with medium-sized flowers in a population near Rinconada, Dpto. La Paz, Bolivia was observed.

Even though a number of species have floral morphologies suggestive of outcrossing, it is clear that there remains a high degree of autogamy in most species. Autogamy is probably the primary means by which populations maintain their distinctness from one another, and it is certainly a strong force in limiting interspecific hybridization. Persistent autogamy does not prevent outcrossing, it merely reduces the frequency of an outcrossing event taking place. While cleistogamy may be the functional mode of pollination in some populations or species, occasional intra- and interspecific crosses between many of these species do occur, providing new genetic variability for segregation and recombination. Even crosses between groups that have developed some internal barriers to hybridization produce occasional fertile seeds that may be capable of surviving. In essence, then, every population is under its own selective pressure, to which it adjusts by reproducing well adapted genotypes and occasionally, through outcrossing, obtains new genetic material.

Ecological relationships. Many South American species of *Epilobium* grow in habitats similar to those in which species in other parts of the world are found; that is, in moist, often disturbed, open sites such as stream banks, ditches, seeps, bogs, lakeshores, etc. Other South American species exhibit a striking amount of ecological specialization, however, which further isolates a number of distinct species. The following list provides a synopsis of the ecological preferences of the various species: *E. australe*, almost always in or near running water, broad elevational range; *E. barbeyanum*, alpine bogs and very wet sites, stems often floating; *E. ciliatum*, any moist, disturbed site, broad elevational range; *E. conjungens*, moist moss mats above timberline; *E. densifolium*, stabilized alpine scree, often away from water, but also along rocky stream banks; *E. denticulatum*, any moist site, broad elevational range; *E. fragile*, moist cracks and crevices in rocks, above 4,500 m; *E. glaucum*, almost always in or near running water, broad elevational range; *E. hirtigerum*, marshes, wet places, mostly at low elevations; *E. nivale*, alpine, along rivulets and other permanently wet spots, up to permanent snow line; *E. pedicellare*, steep or vertical seeps, altiplano; *E. puberulum*, moist disturbed places, mostly at low elevations.

Sympatry. Despite rather strong ecological differences and geographical separations, many species do occur sympatrically, at least in part of their range.

TABLE 8. Sympatric occurrence of native species of *Epilobium* in South America. Acronyms are those given in Table 2. In addition, PED = *E. pedicellare*, FRAG = *E. fragile*, and CONJ = *E. conjungens*. KEY: * = species that occur together and hybridize; + = species that occur together; ? = species that probably occur together.

DENT	.												
PED	*	.											
FRAG	?	.	.										
PUBER									
CIL	*	.	.		*	.							
NIV	+	.						
BARB	*	?	.					
DENS	+	+	?	.				
AUST	*	+	+	*	.			
GLAU	+	.	.	.	+	*	+	*	*	*	.		
CONJ	?	.	.	
HIRTIG	+	*
	DENT	PED	FRAG	PUBER	CIL	NIV	BARB	DENS	AUST	GLAU	CONJ	HIRTIG	

This is especially true in the Andes of central Chile and Argentina at moderate elevation (1,000–1,500 m), where two or more species are often found very near each other, if not intermixed. Up to five species have been seen growing together near the Termas del Río Blanco, Malleco Prov., Chile, at 1,300 m; namely *Epilobium australe*, *E. ciliatum*, *E. densifolium*, *E. glaucum*, and *E. nivale*.

Table 8 summarizes the sympatric occurrence of the native species in South America. The information was obtained primarily from personal observation and mixed herbarium collections, or rarely deduced from locality information. There are a number of combinations that cannot occur because the ranges of the species involved do not overlap. Likewise, there are several sympatric combinations that should occur, but which have not been seen. These are also indicated in Table 8. One of the introduced species, *Epilobium obscurum*, has been found growing mixed with *E. puberulum* and *E. ciliatum*, and is known to hybridize with the latter.

Natural hybridization. The occurrence of natural hybrids has been commented on for many years, beginning with Haussknecht (1884), although the frequency with which they are recognized depends greatly on how finely the species delimitations are drawn. Natural hybrids in *Epilobium* are found throughout the world, although constraints are imposed on their formation by a high degree of autogamy or internal barriers to hybridization.

Very few hybrids have ever been reported from South America, primarily because of the lack of material and field examinations. Samuelsson (1923, 1930) reported hybrids between *E. denticulatum* and *E. hirtum*, now considered to be conspecific, and between *E. denticulatum* and *E. haenkeanum* (= *E. pedicellare*). Only one specimen of the latter combination is now considered to be of hybrid origin, although hybrids between *E. denticulatum* and *E. pedicellare* are difficult to distinguish.

Eleven combinations that are known to form natural hybrids are indicated in Table 8 and documented by specimens whose pollen fertility and seed set have been estimated. These are discussed in detail under the individual species treat-

ments. The majority of natural hybrids have morphology intermediate between the two parents and are often characterized by reduced pollen stainability and seed set. A number of hybrid combinations would be difficult to detect, e.g., *Epilobium australe* \times *E. nivale* or *E. australe* \times *E. densifolium*.

Wherever two or more species occur together hybrids can be formed, but they are relatively infrequent. This, in part, may be due to the ecological distinctness of the habitats in which some species grow, or to other types of barriers to the successful production of hybrid individuals. In contrast to the situation in New Zealand (Raven & Raven, 1976) where hybridization is seen as a central force in the formation of new adaptive genotypes, the South American species, because of their heterogeneous origins, and perhaps the recency of their arrival, have diversified to only a small extent, and not primarily through hybridization.

TAXONOMIC HISTORY

The first botanist to acquire specimens of *Epilobium* from South America was Philibert Commerson, who found *E. hirtigerum* growing near Montevideo, Uruguay, in 1767 when the survey ships *Etiole* and *Boudeuse*, under the command of Louis de Bougainville, stopped on their voyage to the western Pacific. Unfortunately, Commerson died in Mauritius in 1773, before he had a chance to study his collections critically. These were then forwarded to France and incorporated in the collection of the Jardin du Roi.

At this same time, Captain James Cook was also exploring southern South America and the Pacific. With him on his first voyage were the celebrated Joseph Banks and Daniel Solander. Among their many new collections was a second species, *Epilobium australe*, from Tierra del Fuego, collected in 1769.

Somewhat later in the eighteenth century, two major scientific expeditions were financed by the government of Spain, the renowned travels of Hipolito Ruiz, José Pavón, and Joseph Dombey to Peru and Chile (1778–1788), and the Malaspina Expedition, which was sent to survey Spanish territories in the Pacific (1789–1794). During the extensive peregrinations of the former, species of *Epilobium* were encountered in several places, such as Chancay and Tarma, Peru, and Concepción, Chile. The specimens from Peru represented *E. denticulatum*, and those from Concepción were a fourth species, *E. puberulum*. All of these collections, however, were published as *E. denticulatum*, the first name of any South American species to find its way into print (Ruiz & Pavón, 1802).

The Malaspina Expedition was fortunate in having the services of two well trained botanists, Luis Née and Thaddeus Haenke. They prepared many thousands of specimens from South America, Mexico, North America, and the western Pacific. Among these were *Epilobium pedicellare* from Peru collected by Haenke and *E. ciliatum*, *E. glaucum*, and *E. barbeyanum* from Chile, collected by Née. The latter species were most likely acquired when Née left the expedition at Concepción in late 1793 to go overland via Santiago, crossing the Andes to Mendoza and thence across the pampas to Buenos Aires. There, in May 1794, he rejoined the expedition with nearly 10,000 specimens for the return to Spain (Safford, 1905). Unfortunate political circumstances intervened, so that most of the results of the expedition were never published. A set of Haenke's material was sent to Karl Presl in Prague, who later published *E. pedicellare* along with

many other species in his *Reliquiae Haenkeanae* (Presl, 1831). Née's voluminous collections went to the Royal Botanic Garden in Madrid where some plants were eventually described and published, but the majority were not. Thus, by the end of the eighteenth century, eight of the twelve native taxa recognized in this treatment had been collected, but the first name for any of them was not published until 1802.

The time between 1820 and 1870 saw an increasing number of coastal surveys and penetrations of the interior, especially in southern South America. Most notable among the naval surveys were the United States Exploring Expedition under the command of Charles Wilkes (1838–1842), the Antarctic Expedition of James Ross (1839–1842) with J. D. Hooker as botanist, the first voyage of the *Adventure* and *Beagle* under the command of Philip King (1826–1830), and the second voyage of the *Beagle* commanded by Robert FitzRoy, with Charles Darwin as naturalist (1831–1836). At the same time, a substantial number of botanists were spending extended periods of time in limited areas throughout the continent. Those who are especially important to the chronology of South American *Epilobium* were the collecting forays of E. Poeppig, T. Bridges, H. Cuming, C. Gay, and R. Spruce.

During this period of active exploration, there was still a great deal of confusion about the limits of the species. It is not surprising, when one considers the variability of many *Epilobium* species, that the new South American plants could be equated with variable European species (e.g., *E. nivale* with *E. alpinum*, *E. ciliatum* with *E. tetragonum*). J. D. Hooker was quite perplexed by the species of *Epilobium* from the Andes, and considered most of them to be variants of *E. tetragonum*, one of which he felt was sufficiently distinct to be described as a new variety, *E. tetragonum* β *antarcticum* (= *E. australe*) (Hooker, 1847, 1853). Quite frequently South American plants were rather arbitrarily given one of three names, *E. denticulatum*, *E. tetragonum*, or *E. pedicellare*. This state of affairs persisted even to the beginning of the twentieth century, when *E. tetragonum* was still being reported as the name for several different species (Macloskie, 1905; Arechavaleta, 1902).

Carl Haussknecht, beginning with a series of papers in 1879 and culminating in his *Monographie der Gattung Epilobium* in 1884, published many new taxa. He had the advantage of studying the collections of many of the major herbaria of Europe, and thus had more South American material at his disposal than any previous author. Perhaps equally as important was his worldwide familiarity with the genus. He was able to dispel the notion that common European species occurred in southern South America, and he recognized several common taxa as separate species for the first time, e.g., *Epilobium chilense* (= *E. ciliatum*) and *E. australe*. Haussknecht was rather confused by the taxa allied to *E. denticulatum*, but such was the authority of his work that some of his errors were perpetuated, resulting in the report of names such as *E. bonplandianum* and *E. caesium* from central Chile (Reiche, 1898). In total, Haussknecht recognized 18 taxa, representing 9 of the 12 native species presented in this treatment.

Among the most important collections used by Haussknecht in the preparation of the *Monographie* were those of Eduard Poeppig and Rudolfo Philippi. Poeppig made extensive collections in central Chile from 1827 to 1829; R. A. Philippi

arrived there in 1851 with his son Federico, both of whom worked intensively on the flora of Chile for more than 50 years.

Subsequent to Haussknecht's work, R. A. Philippi described seven new species of *Epilobium* (Philippi, 1893) that are here considered conspecific with previously described taxa. Further botanical explorations in Chile and Patagonia during the early years of the twentieth century, especially by Per Dusén and Carl Skottsberg, produced much new material. Among the new species described were *E. barbeyanum* by Lévillé in 1907 and the highly distinctive *E. conjungens* by Skottsberg in 1906.

By 1923, partly under the impetus of a fine set of collections made by Erik Asplund in Bolivia, Gunnar Samuelsson had reviewed the entire genus in South America. He reworked nearly all of the material used by Haussknecht as well as more recent collections. As a result of his studies, he published many new taxa and recognized nearly all of those proposed by Haussknecht, bringing the total number of taxa to 34 species and 10 varieties.

Since that time very little has been published on South American *Epilobium*. Samuelsson, after studying collections in North American herbaria, reduced three taxa to synonymy (Samuelsson, 1930). Other, more recent works by Munz (1933, 1934, 1974), MacBride (1941), and a number of local floras have followed Samuelsson very closely.

SYSTEMATIC TREATMENT

***Epilobium* L., Sp. Pl. 347. 1753, Gen. Pl., ed. 5, 164. 1754. LECTOTYPE: *Epilobium hirsutum* L., Britton & Brown, Ill. Fl. No. U.S. & Can., ed. 2, 2:590. 1913. (Complete synonymy not given.)**

Chamaenerion Séguier, Pl. Veron. 3:168. 1754. LECTOTYPE: *Epilobium hirsutum* L., Holub, Folia Geobot. Phytotax. 7:84. 1972.

Zauschneria Presl, Rel. Haenk. 2:28, pl. 52. 1831. TYPE: *Z. californica* Presl.

Chamerion (Raf.) Raf., Herb. Raf. 51. 1833. Based on *Epilobium* subgen. *Chamerion* Raf., Amer. Monthly Mag. & Crit. Rev. 2:266. 1818. TYPE: *E. amenum* Raf.

Crossostigma Spach, Ann. Sc. Nat. Bot., ser. 2, 4:174. 1835. TYPE: *C. lindleyi* Spach, nom. illeg. = *E. minutum* Lindl. ex Lehm.

Pyrogennema Lunell, Amer. Midl. Naturalist 4:482. 1916. TYPE: *P. angustifolium* (L.) Lunell.

Cordylophorum (Nutt. ex Torr. & Gray) Rydb., Fl. Rocky Mts. 590, 1064. 1917. Based on *Epilobium* sect. *Cordylophorum* Nutt. ex Torr. & Gray, Fl. N. Amer. 1:488. 1840. TYPE: *C. suffruticosum* (Nutt.) Rydb.

Erect or creeping perennial or annual (3 species) herbs, sometimes woody at the base, overwintering and reproducing vegetatively by loose, scaly rhizomes, stolons, buds in the axils of leaves, soboles, leafy rosettes, or turions (fleshy, scale-leaved buds produced at or below the ground surface). Leaves simple, petiolate or sessile, opposite, at least at the lower nodes, alternate above, or all opposite, or all alternate in sect. *Chamaenerion*; pubescent or glabrous, the pubescence often distributed in descending lines on raised decurrent petiole margins. Flowers actinomorphic, or slightly zygomorphic in a few species, solitary in the axils of more or less reduced or unmodified leaves, clustered upwards, usually forming a few- to many-flowered, more or less discrete racemose, paniculate, or corymbose inflorescence, or scattered and few. Floral tube present or absent (sect. *Chamaenerion*). Sepals 4. Petals 4, white, cream, pink to rose pur-

ple, red, or yellow, emarginate or cleft. Stamens 8, the 4 antisepalous ones longer than the 4 antipetalous ones. Stigma capitate, clavate or deeply 4-lobed, protandrous or protogynous, or the anthers dehiscing at about the same time that the stigma becomes receptive. Capsule narrow, elongate or rarely narrowly clavate, 4-locular, loculicidal. Seeds many or rarely one or two in each locule, mostly obovoid, with a coma of long silky hairs at the chalazal (terminal) end that is rarely absent (1 species and some populations of a second). Gametic chromosome numbers: $n = 12, 13, 15, 16$, and 18 , with polyploidy based on 15 and 18 in some taxa.

The generic description is based on the genus worldwide. As a result, some of the features given are not present in any of the South American species. The interested reader should refer to Raven (1976) and references therein for complete descriptions, discussion of generic and sectional delimitations, and synonymy.

Since it is now fairly well understood that the *Epilobium* species that occur in South America have had various and diverse origins, the arrangement of the taxa in a systematic treatment cannot be purely evolutionary. Instead, the species have been placed in what I believe to be more or less phyletic groups, beginning with those having the AA chromosomal arrangement, endemic and native, then the BB, endemic and native, and then those that have been introduced recently. *Epilobium paniculatum*, in sect. *Xerolobium*, by virtue of its primitive or distinctive features and lower chromosome number, might have been placed first. Because it is only sparingly introduced in South America, however, it has been placed at the end with the other introduced species. Neither descriptions nor keys have been prepared to distinguish the sections of *Epilobium*.

There are several points that must be kept in mind in order to understand fully the nature of the taxa enumerated here. Often there are great differences in the seasonal aspect of the plants. Those collected at the end of a growing season may be more branched, with few, often withered, lower leaves; and the flowers, fruits and seeds are often smaller than those produced by the same plant earlier in the season. Overwintering structures such as turions are frequently produced only near the end of a growing season, and may not be present. Or, as is often the case, specimens have been collected without regard to underground parts, even though they are taxonomically useful. Seeds from old or well dried specimens may be 10% smaller in both length and width than fresh, mature seeds (Raven & Raven, 1976). The dimensions given in the descriptions attempt to cover the full range of dry and fresh seeds.

Our understanding of the role of populations as evolutionary units has tended to broaden our view of what constitutes a species. In fact, considering the highly autogamous nature of most epilobiums, it is extremely questionable whether one can speak of more than a single plant as an evolutionary unit (Ehrlich & Raven, 1969; Levin & Kerster, 1974; Raven & Raven, 1976). Hence, the concept of a species or other taxon must be painted with a rather broad brush for it to be of any practical utility. This is fundamentally different from the approach taken in earlier times when many of the taxa in *Epilobium* were first given recognition. Plants that were at one time thought to be taxonomically distinct, I here may consider to be only a part of the "normal" variation within a polymorphic species or even a single population.

The descriptions and discussions have taken into account nearly all of the available herbarium material. With the exception of *E. conjungens* and *E. fragile*, all of the native species have been studied in the field, and one or more strains of each have been grown in greenhouses at the Missouri Botanical Garden.

A note of special significance for the nomenclature concerns the formae that Haussknecht used in his *Monographie* (Haussknecht, 1884). According to Raven (1962), the use of the feminine ending suggests that Haussknecht thought of his formae simply as organizational devices for the presentation of variation, and not as formal taxonomic units. Following this convention, the formae have been included in the synonymy only when they were taken up by later authors.

In the specimens examined, collections from Chile are placed in regions and provinces according to the most recent Atlas published by IGM (Instituto Geográfico Militar, 1980). This atlas follows the regionalization system implemented in 1973, which divided the country into 13 regions and 50 provinces. Specimens from other countries are placed according to the most recent maps available.

KEY TO THE SPECIES OF *EPILOBIUM* IN SOUTH AMERICA

- 1a. Stems creeping, growing and rooting beyond the region of flower production, leaves all opposite; flowers few and scattered. Tierra del Fuego and adjacent islands. ----- 12. *E. conjungens*
- 1b. Stems not creeping, erect, ascendent or decumbent, not growing and rooting beyond the flowers; leaves at least partly alternate; flowers few to many, in a more or less discrete inflorescence.
 - 2a. Seeds broadly obovoid with a conspicuous constriction toward the micropylar end; floral bracts minute, fused to the pedicel; leaves often conduplicate, early deciduous, mostly alternate; annual. Western Neuquén and Chubut, Argentina. ----- 15. *E. paniculatum*
 - 2b. Seeds variously shaped, but without a conspicuous constriction; floral bracts leaf-like, reduced or not, but not fused to the pedicel, leaves flat, persistent, alternate or opposite; perennial, but usually flowering the first year.
 - 3a. Plants glabrous (very rarely plants of *E. ciliatum* glabrous, but immediately distinguishable by their turions and longitudinally ridged seeds). Andes of Chile and Argentina.
 - 4a. Plants low, caespitose; stems decumbent; leaves acute or obtuse, not glaucous. ----- 6. *E. nivale*
 - 4b. Plants robust, loosely rhizomatous, more or less clumped; stems erect; leaves acuminate, glaucous. ----- 10. *E. glaucum*
 - 3b. Plants variously pubescent, the hairs sometimes very sparse or restricted to the junction of the petiole bases.
 - 5a. Upper stems hirsute or villous, and glandular, the hairs erect or slightly spreading.
 - 6a. Leaves mostly alternate, opposite only at the lowest few nodes, coarsely serrate; inflorescence erect; petals white. Southern Brazil, Uruguay, eastern Argentina. ----- 11. *E. hirtigerum*
 - 6b. Leaves mostly opposite, alternate or subopposite only above or in the inflorescence, denticulate; inflorescence usually nodding; petals pink. Andes, Costa Rica to northern Chile and Argentina. ----- 1. *E. denticulatum*
 - 5b. Upper stems variously pubescent, but not hirsute or villous, the hairs not erect.
 - 7a. Stems and ovaries densely erect glandular throughout, with some strigillose hairs; largest leaves with 3–5 teeth on each side; plants soboliferous or stoloniferous; seeds papillose. Central Andes of Chile and Argentina. ----- 7. *E. barbeyanum*
 - 7b. Stem and ovary pubescence various, if densely glandular then the leaves with more than 6 teeth on each side, or plants not soboliferous or stoloniferous; seeds variously sculptured.

- 8a. Leaves mostly alternate, opposite only at the lowest one or two nodes, or on very young shoots, coarsely and irregularly doubly serrate with uneven-sized teeth. Peru and Bolivia. 2. *E. pedicellare*
- 8b. Leaves mostly opposite or subopposite, alternate only above or in the inflorescence, denticulate or once serrate.
 - 9a. Stems nearly glabrous, the pubescence a few scattered hairs, mostly at the fused petiole bases; plants low, <15 cm, densely caespitose. Peru, Bolivia and Chile. 3. *E. fragile*
 - 9b. Stems variously pubescent, the pubescence more or less dense throughout; plants various.
 - 10a. Plants densely caespitose, usually <15 cm tall, with a woody, contorted rootstock; flowers large, the petals 7–12 mm long; seeds 1.4–2.0 mm long. Central Andes of Chile and Argentina. -- 8. *E. densifolium*
 - 10b. Plants loosely clumped or solitary, usually >15 cm tall; flowers large or small; seeds less than 1.4 mm long.
 - 11a. Leaves narrowly ovate to ovate, thick, coarsely serrate with 4–8(–12) teeth on each side; plants not glandular. Andes of Chile and Argentina. 9. *E. australe*
 - 11b. Leaves narrowly lanceolate to lanceolate, serrulate or denticulate, or if narrowly ovate, then the inflorescence glandular.
 - 12a. Floral tube with a few, erect, glandular hairs, otherwise the plants not glandular (rarely also with a few on the upper portion of the ovary); largest leaves usually with 10 or more low denticulate teeth on each side; inflorescence erect. Central Chile. 13. *E. obscurum*
 - 12b. Floral tube not glandular, or if glandular, then the glandular hairs also found on other plant parts, or minute and appressed; leaf margins various; inflorescence erect or nodding.
 - 13a. Leaves serrulate, the largest usually with 10 or more teeth on each side, acuminate, the blade glabrous above and below; plants producing leafy rosettes or fleshy turions, the turions often persisting as a cluster of dead scales at the base of the stem.
 - 14a. Seeds with longitudinal rows of flattened, fused papillae, at least along the sides; inflorescence glandular; lower stem smooth. Chile and Argentina. 5. *E. ciliatum*
 - 14b. Seeds papillose, the papillae distinct; inflorescence not glandular; lower stems often with exfoliating epidermis. Central Chile. 14. *E. tetragonum*
 - 13a. Leaves denticulate, acute or obtuse, usually with fewer than 10 low teeth on each side, if more than 10, then the inflorescence nodding, the blade more or less pubescent, the

hairs sometimes minute and appressed; plants without turions or basal rosettes, soboliferous or with leafy basal shoots.

- 15a. Stems with raised decurrent lines from the margins of the petioles; inflorescence and flowers nodding; younger leaves and upper stems usually with appressed to erect glandular or blunt-tipped hairs under higher magnification; petals pink to rose purple. Andes, Costa Rica to northern Chile and Argentina. ----- 1. *E. denticulatum*
- 15b. Stems without raised decurrent lines from the margins of the petioles; inflorescence erect; leaves and stems not glandular; petals salmon pink. Central Chile. -----
----- 4. *E. puberulum*

1. ***Epilobium denticulatum*** Ruiz & Pavón, *Flora Peruviana et Chilensis* 3:78, *tab.* 314, *f.* 1–1a. 1802. TYPE: Perú, Dpto. Junín, Tarma, 1779–1781, *H. Ruiz & J. Pavón* (MA, lectotype here designated, photograph MO; B (destroyed, photographs BH, MO), BM, F, G, OXF, isoelectotypes). De Candolle, *Prodromus* 3:42. 1828. Hausskn., *Monogr. Epilobium* 264. 1884. Samuelsson, *Svensk Bot. Tidskr.* 17:250. 1923. MacBride, *Field Mus. Nat. Hist., Bot. Ser.* 8(4):530. 1941. Munz, *Opera Bot. Ser. B*, 3:6. 1974.

E. bonplandianum H.B.K., *Nov. Gen. et Spec. Plant.* 6:95. 1823. TYPE: Colombia, Dpto. Cauca, Andes de Popayán, Páramo de Puracé, 2,900 m, November–December 1801, *A. Humboldt & A. Bonpland s.n.* (P, lectotype here designated, photograph MO; P, isoelectotype, photograph GH; F, HAL, P, probable isoelectotypes). Humboldt & Bonpland, *Synop. Plant. Aeq.* 3:389. 1824. Hausskn., *Monogr. Epilobium* 267. 1884.

E. junceum Forst. f. ex Spreng., *Syst. Veg.* 2:233. 1825, nom. illegit. Based on *E. denticulatum* Ruiz & Pavón.

E. pedicellare auct. non Presl: Hook. & Arn., *Bot. Misc.* 3:309. 1833, pro parte.

E. caesium Hausskn., *Oesterr. Bot. Z.* 29:91. 1879. TYPE: Bolivia, Dpto. La Paz, Prov. Caupolicán, Pelechuco, 3,900–4,200 m, March 1865, *R. Pearce s.n.* (K, holotype, photograph MO). Hausskn., *Monogr. Epilobium* 268, *tab.* 17, *f.* 75, 75a–c. 1884.

E. andicolum Hausskn., *Oesterr. Bot. Z.* 29:118. 1879. TYPE: Bolivia, Dpto. La Paz, Prov. Larecaja, vicinity of Sorata, 1859, *M. G. Mandon 626* (K, lectotype here designated, photograph MO; BM, BR, GOET, K, P, isoelectotypes). *Mandon 626* is apparently a distribution number. From an examination of the many sheets available, it is probable that several gatherings were included. The lectotype and isoelectotypes are limited to those specimens annotated as *E. andicolum* by Haussknecht. Hausskn., *Monogr. Epilobium* 266, *tab.* 17, *f.* 76, 76a–c. 1884. Samuelsson, *Svensk Bot. Tidskr.* 17:255. 1923; *Svensk Bot. Tidskr.* 24:2. 1930.

E. meridense Hausskn., *Oesterr. Bot. Z.* 29:148. 1879. TYPE: Venezuela, Est. Mérida, Sierra Nevada, 3,300 m, August 1842, *J. Linden 418* (W, lectotype here designated, photograph MO; BM 2 sheets, BR (probable), F, G (photographs BH, MO), K, OXF, P 2 sheets, TCD, W, isoelectotypes). Hausskn., *Monogr. Epilobium* 266. 1884. H. Lév., *Iconogr. Epilobium tab.* 193, 194. 1911. Samuelsson, *Svensk Bot. Tidskr.* 17:257. 1923; *Svensk Bot. Tidskr.* 24:9. 1930. Munz, *Aliso* 4:488. 1960; *N. Amer. Fl.* II 5:218. 1965; *Opera Bot., Ser. B*, 3:7. 1974. Vareschi, *Flora de Los Páramos* 247, *f.* 77. 1970.

E. helodes H. Lév., *Bull. Herb. Boissier, sér.* 2, 7:589. 1907. TYPE: Colombia, Dpto. Tolima, Páramo de Ruiz, high montane forest, 3,000 m, 11 September 1883, *F. C. Lehmann 3158* (G, holotype, photograph MO; BM, US, isotypes). *E. meridense* var. *helodes* (H. Lév.) Samuelsson, *Svensk*

- Bot. Tidskr. 17:258. 1923. Samuelsson, Svensk Bot. Tidskr. 24:10. 1930. Munz, Opera Bot., Ser. B, 3:7. 1974.
- E. denticulatum* var. *aberans* Samuelsson, Svensk Bot. Tidskr. 17:253. 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Aberoa, Challapata, 3,750 m, 31 March 1921, *E. Asplund* 3250 (UPS, holotype, photograph MO; S, isotype).
- E. denticulatum* var. *confertum* Samuelsson, Svensk Bot. Tidskr. 17:252. 1923. TYPE: Ecuador, Prov. Pichincha, Quito, 1847, *W. Jameson* 192 (W, lectotype, photograph MO; BM, G, S, TCD, US, isolectotypes; P. Munz, Opera Bot., Ser. B, 3:6. 1974).
- E. denticulatum* var. *macropetalum* Samuelsson, Svensk Bot. Tidskr. 17:253. 1923. TYPE: Perú, Dpto. Cuzco, Pacechac, near Río Urubamba, 4,500 m, 3 March 1903, *A. W. Hill* 155 (K, lectotype; P. Munz, Opera Bot., Ser. B, 3:6. 1974).
- E. asplundii* Samuelsson, Svensk Bot. Tidskr. 17:256, *tab. 3, f. 2*. 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Omasuyos, Challa, Isla del Sol, 3,850 m, 18 April 1921, *E. Asplund* 3708 (UPS, holotype, photographs MO, S).
- E. meridense* var. *condensatum* Samuelsson, Svensk Bot. Tidskr. 17:258. 1923. TYPE: Ecuador, Prov. Chimborazo, El Altar, 3,900–4,000 m, July 1903, *H. Meyer* 174 (JE, lectotype here designated, photograph MO; JE, isolectotype). All of the material cited by Samuelsson was located at Berlin (B) and is now destroyed. The lectotype has been selected from the duplicates of that material at other institutions.
- E. aequinoctiale* Samuelsson, Svensk Bot. Tidskr. 17:259, *tab. 2, f. 1*. 1923. TYPE: Colombia, Dpto. Nariño, Túquerres, 1844–1847, *H. Karsten* (W, lectotype here designated, photographs BH, MO, S; JE, isolectotype). *H. Lév.*, Iconogr. *Epilobium* *tab. 198* (as *E. repens*). 1911. Munz, Opera Bot., Ser. B, 3:4. 1974.
- E. assurgens* Samuelsson, Svensk Bot. Tidskr. 17:261, *tab. 5, f. 2*. 1923. TYPE: Ecuador, Prov. Tunguragua, Volcán Tunguragua, "Locis paludosis," May 1858, *R. Spruce* 5389 (W, lectotype here designated, photographs BH, MO, S; BM, K 2 sheets, NY, OXF, TCD, W, isolectotypes). Samuelsson, Svensk Bot. Tidskr. 24:3. 1930.
- E. bolivianum* Samuelsson, Svensk Bot. Tidskr. 17:263, *tab. 2, f. 3*. 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Murillo, stream at La Cumbre, 4,600 m, 26 May 1921, *E. Asplund* 4014 (UPS, holotype, photographs MO, S; B (destroyed, photographs BH, MO, US), S, W, Z, isotypes). MacBride, Field Mus. Nat. Hist., Bot. Ser. 8(4):530. 1941.
- E. deminutum* Samuelsson, Svensk Bot. Tidskr. 17:264, *tab. 4, f. 5*. 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Murillo, Nevado Huayna-Potosí, Glaciar Franz Josefs, *Germann* 24 (W, holotype, photographs BH, MO, US, fragment UPS). Samuelsson, Svensk Bot. Tidskr. 24:5. 1930.
- E. hirtum* Samuelsson, Svensk Bot. Tidskr. 17:266, *tab. 2, f. 2*. 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Murillo, San Jorge, now within the city of La Paz, 3,500 m, 1 November 1920, *E. Asplund* 666 (UPS, lectotype here designated, photographs MO, S; S, isolectotype). Samuelsson, Svensk Bot. Tidskr. 24:4. 1930. MacBride, Field Mus. Nat. Hist. Bot. Ser. 8(4):532. 1941.

Variable, clumped perennial herbs (10–)20–70(–160) cm tall, reproducing vegetatively by elongate, leafy shoots or soboles produced at or near the base. Stems erect or ascendent, several to many, mostly simple, occasionally branched above, and often from the base, strigillose to spreading hirsute, with hairs 0.1–0.4 mm long, often with an admixture of appressed to erect glandular hairs, 0.05–0.2 mm long, at least in the inflorescence. Leaves mostly opposite, alternate above and in the inflorescence, thin, green, occasionally reddish purple, especially along the veins and margins, lanceolate, occasionally ovate, rarely broadly so, 1–5.6 cm long, 0.2–1.7 cm wide, acute to acuminate, rarely obtuse at the apex, denticulate with 3–8(–13) low teeth on each side, acute to cuneate, occasionally obtuse or rounded at the base, strigillose to spreading hirsute on the abaxial and adaxial veins and midrib, or thinly scattered on the blade, with scattered appressed to spreading blunt-tipped or glandular hairs, 0.05–0.2 mm long, occasionally densely so, the lateral veins prominent, 2–4(–5) on each side of the midrib, on petioles 0.5–2(–4) mm long, rarely sessile. Inflorescence simple, nodding, the leaves subtending the flowers usually slightly reduced in size. Flowers nodding at anthesis. Ovaries often reddish or purplish, strigillose to spreading hirsute, often densely so, usually with an admixture of appressed to spreading glandular hairs, 0.9–2.2

cm long, on pedicels 2–5(–8) mm long. Floral tube often reddish purple, 0.8–2 mm deep, 1.5–3(–4) mm across, externally strigillose to spreading hirsute, usually with appressed to spreading glandular hairs, internally with a ring of erect villous hairs 0.1–0.2 mm long, sometimes reduced to only a few, or occasionally glabrous. Sepals often reddish purple, lanceolate, 2.2–5.7(–7) mm long, 1.1–2.1 mm wide, strigillose to spreading hirsute, usually with appressed to spreading glandular hairs. Petals pale pink to rose purple, occasionally white or nearly so, obovate, rarely broadly so, (2.5–)3.5–7.6(–9.5) mm long, (2–)2.7–4(–6.1) mm wide, the notch 1.1–2 mm deep. Anthers cream to white, or slightly pinkish, 0.6–1.6 mm long, 0.4–0.9 mm wide; filaments bluish purple to pale lavender, those of the longer stamens (1.4–)1.8–3.2(–4.4) mm long, those of the shorter (0.7–)1.5–2.8(–3.2) mm long; the longer stamens, and often the shorter, shedding directly on the stigma at anthesis, or held away and bending toward the stigma after anthesis in some populations. Style white to slightly bluish, (2.2–)3.5–6.3(–9) mm long; stigma white, capitate to clavate, 1.1–2 mm long, 0.8–1.2 mm thick, occasionally exerted beyond the anthers. Capsules erect, strigillose to spreading hirsute, usually with appressed to erect glandular hairs, often glabrate or glabrous, 3.5–7(–8.5) cm long, 1.3–1.7 mm thick, on pedicels 0.3–2.5(–3.4) cm long. Seeds brown, papillose, obovoid, 0.8–1.1 mm long, 0.35–0.45 mm thick, the chalazal end with a short appendage, 0.04–0.1 mm long, 0.08–0.14 mm wide; coma white to slightly yellowish, 4–7 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 1): A widespread, weedy species that grows along stream banks, seeps, bogs, moist embankments, roadsides, or other open disturbed sites, mostly in the páramos and puna of the high Andes but also extends into forested zones. In South America throughout the northern and central Andes from the páramos of Venezuela and Colombia, including the Sierra de Santa Marta and the Sierra de Perijá, southward through Ecuador; widely distributed in the altiplano of Perú, Bolivia, northeastern Chile, and northwestern Argentina, continuing southward along the eastern side of the Andes to central Mendoza Prov., Argentina; disjunct in the Sierra de San Luis and the Sierra Grande de Córdoba. In North America restricted to the Sierra de Talamanca, Costa Rica. Found growing between 2,500 and 4,800 m throughout most of its range, descending to lower elevations along roads in forested zones, or along rivers in drier areas; at its southern limit typically between 1,800 and 3,000 m, and in the Sierra Grande de Córdoba between 1,200 and 2,500 m. Flowering throughout the year from Venezuela to Peru; however, from Bolivia southward there is a marked suppression of flowering during the coldest, driest months (July and August in Bolivia) and therefore in the southernmost parts of its range, flowering occurs between December and March.

Representative specimens examined: ARGENTINA, CATAMARCA: Dpto. Ambato, Sierra de Ambato, Casa de Cubas, 3,000 m, *Hunziker & DeFulvio* 19828 (CORD, MO); Dpto. Pomán, Las Casitas, Sierra de Ambato, 2,500 m, *Hunziker & Ariza* 20424 (CORD, MO); Dpto. Capayán, Los Angeles, *Russo* 792 (LIL); Belén, Quebrada de Los Potrerillos, 2,600 m, *Sleumer & Vervoorst* 2461 (US). CÓRDOBA: Dpto. San Javier, Quebrada del Tigre, 1,800 m, *Bridarolli* 1440 (LP); Pampa de Achala, Los Gigantes, *Castellanos in* 1924 (BA); Sierra Achala, Cuesta de La Sala Grande, *Hieronymus* 856 (CORD, F, US); Sierra Grande, Cuesta de Copina, *Hunziker* 8738 (CORD, MO, RSA); Sierra Grande, E slope Cerro Champaqui, *Hunziker* 9618 (CORD, MO, RSA); La Cumbrecita, 1,450 m, 31°55'S, 64°15'W, *Solomon* 4192 (MO). JUJUY: Dpto. Yavi, Quebrada de Toquero, 3,600 m, 22°18'S, 65°36'W, *Cabrera et al.* 15380 (BAB, LP, M); Dpto. Tumbaya, Volcán Chilcayo, 23°43'S, 65°40'W, *Fabris et al.* 6290



FIGURE 1. Distribution of *Epilobium denticulatum*.

(LP). Dpto. Tilcara, Quebrada del Abra de la Cruz, *Fabris et al.* 6353 (BAA, LP); Dpto. Valle Grande, Caspalá, 3,000 m, 23°19'S, 65°08'W, *Fabris & Crisci* 6925 (LP); Dpto. Tumbaya, Angosto del Chañi, 3,900 m, *Kiesling et al.* 298 (LP); Dpto. Humahuaca, Río Despensas, 4,000 m, *Ruthsatz IV60* (BAA, MO). LA RIOJA: Dpto. Famatina, Los Corrales, *Cabrera et al.* 27254 (BAB, SI); Dpto. Famatina, Sierra Famatina above La EnCrucijada, 3,200 m, 28°58'S, 67°42'W, *Hawkes et al.* 3404 (C); Sierra de

Famatina, Cueva de Medina, 3,100 m, *Krapovickas 6163* (BAB, CORD). MENDOZA: Quebrada de Alvarado, 3 km S of Chilicito, 1,550 m, *Hjerting 6322* (C); Dpto. Tunuyán, 10 km W of Campo de Los Andes, 1,500 m, *Melis & Barkley in 1950* (LIL); Dpto. Tupungato, Río La Carrera, 2,350 m, *Sleumer 427* (B). SALTA: Dpto. Calayate, Sierra de Los Quilmes, 2,400 m, *Castellanos in 1943* (BA, RSA); Nevado Castillo, 25°11'S, 65°21'W, *Lorentz & Hieronymus 88* (CORD, F, GOET, JE, S, US); Dpto. Guachipas, Pampa Grande, 1,600 m, 25°40'S, 65°30'W, *Hunziker 1820* (POM); Dpto. Santa Victoria, Santa Victoria, 2,385 m, *Meyer 4962* (F, UC). SAN JUAN: Dpto. Iglesia, Cordillera Agua Negra, Piedras Negras, 30°16'S, 69°47'W, *Castellanos in 1950* (US); Dpto. Iglesia, Vega de Santa Rosa, 3,300 m, 29°00'S, 69°15'W, *Hunziker & Caso 4791* (BAB, CORD); Cienaga de Las Cabeceras, 2,700 m, 31°47'S, 69°07'W, *Kurtz 9808* (BAF, CORD). SAN LUIS: Pancanta, 32°59'S, 66°11'W, *Castellanos in 1925* (BA); Sierra de San Luis, Arroyo de Las Aguilas, *Vignati 101* (LP). TUCUMÁN: Dpto. Tafi, Lara, 3,200 m, *Rodríguez 310* (BA, BAF, GH, MO, RSA, S, SI); Dpto. Chicligasta, Estancia Las Pavas, Río Cascada, 2,700 m, *Venturi 3033* (BA, BAB, DS, GH, MO, SI); Dpto. Tafi, Cerro San José, 2,700 m, *Venturi 3573* (BA, BAB, DS, GH, RSA, SI, US); Dpto. Chicligasta, Estancia Santa Rosa, 3,300 m, *Venturi 4787* (BA, BAB, LP, MO, SI).

BOLIVIA, COCHABAMBA: Cona-Cona, 4,000 m, 18°00'S, 66°45'W, *Brooke 5181* (BM); Vila-vila, 18°00'S, 65°30'W, *Brooke 5859* (BM, F, NY); Between Chimore and Cochabamba, Km 80, 3,000 m, 16°42'S, 64°49'W, *Cárdenas 760* (LIL, US). Prov. Ayopaya, Sailapata, 2,700 m, 16°30'S, 66°35'W, *Cárdenas 3057* (BR, F, P, S, US). Prov. Cercado, Sierra Tunari near Lago Huara-Huara, 17°12'S, 66°10'W, *Hawkes & Hjerting 6606* (C, MO). Prov. Quillacollo, 28 km from Quillacollo on road to Morochata, 3,850 m, 17°19'S, 66°22'W, *Hawkes & Hjerting 6692* (C). 35 km W of Comarápa on road to Cochabamba, 2,700 m, *King & Bishop 7654* (MO, US). Prov. Carrasco, 2 km above Siberia, 3,200 m, *Steinbach 210* (F, GH, MO, NY, US, WIS). Prov. Ayopaya, Puente San Miguel, 25 km NNW of Cochabamba, 3,800 m, 17°10'S, 66°25'W, *Ugent 4781* (DS, GH, MSC, UC, US, WIS). LA PAZ: Prov. Murillo, entre Pongo and La Rinconada, 4,000 m, *Asplund 1818* (S, UPS). Prov. Ingavi, Guaqui, *Asplund 2305* (S, UPS, Z). Prov. Pacajes, General Campero, 3,900 m, 17°27'S, 68°58'W, *Asplund 2791* (UPS). Prov. Omasuyos, Isla del Sol, Challa, 3,850 m, *Asplund 3709* (S, UPS). Vicinity of La Paz, 3,000 m, *Bang 75* (E, G, GH, MO, NY, PH, US). Prov. Murillo, Palca, 5 km hacia la mina San Francisco, 4,800 m, *Beck 2223* (MO). Prov. Ingavi, Huacullani, 3,840 m, *Beck 2470* (MO). Mina La Fabulosa, 4,600 m, 16°00'S, 68°00'W, *Brooke 6329* (BM, NY). La Paz, *Buchtien in 1919* (ARIZ, BM, BP, C, LD, E, F, G, GH, M, MO, NY, S, US, Z); *in 1930* (BM, C, E, G, K, M, MO, S, Z). 30 km SW of Yoloso on road to Unduavi, 2,900 m, *Davidson 4968* (LAM). Prov. Larecaja, vicinity of Sorata, *Mandon 626* (F, G, GH, GOET, JE, MICH, MO, MPU, NY, PR, S, US, W); *Williams 1549* (BM, NY). Yungas, 1,800 m, *Rusby in 1885* (F, GH, MICH, NY, PH, US, WIS). Valle de Hichucota, Laguna Kkota, 4,500 m, 16°07'S, 68°20'W, *Solomon 4938* (MO). Valle de Hichucota, 4,150 m, *Solomon 5007* (MO); 11.3 km NE of La Paz on road to Unduavi, 4,400 m, *Solomon 5013* (MO). La Cumbre on road to Unduavi, 4,600 m, 16°20'S, 68°03'W, *Solomon 5028* (MO). 6 km W of Palca on Placa-La Paz road, 3,800 m, 16°32'S, 67°58'W, *Solomon 5139* (MO). Upper Valle de Zongo, 3,000 m, 16°10'S, 68°09'W, *Solomon 5243* (MO). Prov. Murillo, Valle de Achocalla, 3,800 m, 16°35'S, 68°11'W, *Solomon 5298* (MO). POTOSÍ: Between Quechisla and Chorolque, 3,600 m, 20°56'S, 66°01'W, *Cárdenas 304* (US). Lagunillas, 3,800 m, *Cárdenas 410* (US). SANTA CRUZ: Near Valle Grande, 2,600 m, *Cárdenas 5138* (US). TARIJA: Iscayache, 3,600 m, *Fiebrig 3015* (BM, E, G, CH, GOET, L, M, P, PR, PRC, S, US, W). Rincón de la Victoria, 17 km W of Tarija, *Krapovickas et al. 18880* (CTES).

CHILE, I REGIÓN (TARAPACÁ): Arica, Camino de Arica al Portezuelo de Chapiquiña, Km 99, 3,500 m, 18°19'S, 69°31'W, *Martcorena et al. 59* (CONC, MO), 98 (CONC); Al interior de Chitita, 2,500 m, 18°49'S, 69°41'W, *Schlegel 5100* (MO). Iquique, Al interior de Coscaya, 3,360 m, 19°51'S, 69°09'W, *Ricardi et al. 418* (CONC, MO); Quebrada de Quipisca, Noasa, 3,500 m, 19°59'S, 67°08'W, *Werdermann 1060* (BM, CAS, E, F, G, GH, LIL, MO, NY, S, SI, U, UC, US, Z); Chusmiza, 19°41'S, 69°11'W, *Zöllner 2947* (MO). Parinacota, Socoroma, 3,300 m, 18°15'S, 69°37'W, *Richard et al. 190* (CONC, MO). II REGIÓN (ANTOFAGASTA): Antofagasta, Sierra Almeida, Aguada Chocas, 3,700 m, 24°15'S, 68°35'W, *Biese 2337* (LIL), 2388 (LIL). El Loa, Caspana, 22°20'S, 68°14'W, *Mahu in 1969* (LD); Toconoa, 23°11'S, 68°01'W, *Pfister in 1950* (CONC).

COLOMBIA, ANTIOQUIA: Páramo Frontino, Cerro de Campanas, 3,650 m, 6°28'N, 76°04'W, *Boeke & McElroy 302* (MO, NY). BOYACÁ: Sierra Nevada del Cocuy, Laguna de San Pablo, 3,850 m, *Grubb et al. 107* (COL, K, MSC, US); Quebrada Surbar, between Duitama and Charalá, 3,273 m, *Langenheim 3537* (COL, UC, US). CALDAS: Nevado del Ruiz, entre Termas y Líbano, *Barclay & Juajibioy 6380* (COL, MO, RSA); Pinares, above Salento, 2,800 m, *Pennell 9347* (GH, NY, PH, US); Páramo del Quindo, 3,700 m, *Pennell & Hazen 9989* (GH, NY, PH, S, US, WU). CAUCA: Between Guachicono and Río Putis, 2,500 m, *Core 933* (RSA, US); Páramo de Las Papas, El Boquerón, *Idrobo et al. 3014* (COL); San Antonio, 2,300 m, *Pennell 7653* (GH, NY, PH, US); Entre Popayán y Puracé, Río Anambio, 2,500 m, *Pérez & Cuatrecasas 5869* (COL, US). CUNDINAMARCA: 15 km N of Usaquén, 2,600 m, *Haught 6205* (COL, US); 20 km NE of Bogotá, 2,470 m, *Luteyn et al. 4809* (COL, F, MO, NY, US); Zipaquirá, 2,650 m, *Pennell 2542* (F, GH, MO, NY, US). HUILA: Moscopán, Santa Leticia,

2,230 m, *Garcia-Barriga & Hawkes 12893* (COL, LIL, RSA, US); Balsillas, on Río Balsillas, 2,000 m, *Rusby & Pennell 728* (F, GH, MO, NY, US). MAGDALENA: Sierra Nevada de Santa Marta, Hoya del Río Donachuí, 3,600 m, *Cuatrecasas & Castañeda 24538* (COL, US); Sierra de Santa Marta, Paso de Mamancanaca-Cambiremena, 3,800 m, *Weston 10391* (MO). META: Páramo de Sumapaz, 4,100 m, *Cleef 7987* (COL, MO); Río Arroz above Quebrada Pedregal, 3,445 m, *Fosberg 20911* (RSA, US). NARIÑO: 31 km E of Pasto on road to Sibundoy, *Berry 3253* (MO); Volcán Galera, Hacienda Obonuco, *Espinosa 2777* (CAS, DS, RSA); Volcán de Cumbal, near Laguna Bolsa, 2,930 m, *Ewan 16138* (BM, POM, RSA, US); Páramo del Támano-Putúm, *Garcia-Barriga 4552* (COL); Camino de Túquerres a La Chorrera, 3,000 m, *Mora 755* (AAU, COL). NORTE DE SANTANDER: Valley of Río Chitaga, SW of Pamplona, 2,600 m, *Fassett 25958* (RSA, US); Laso, N of Toledo, 2,400 m, *Killip & Smith 20391* (F, GH, NY, S, US). PUTUMAYO: Valley of Sibundoy, Portachuelo, 2,400 m, *Schultes & Villarreal 7736* (COL, ECON, F, GH, US); Between La María and Páramo de San Antonio, 2,900 m, *Schultes & Villarreal 7832* (COL, GH, LIL, US); Páramo de Quilisayaco, 3,300 m, *Uribe 5380* (COL, NY). SANTANDER: Berlín, 3,100 m, *Enrique et al. 577* (COL, MO); Páramo de Las Vegas, 3,300 m, *Killip & Smith 15715* (BM, F, GH, NY, P, S, US); Páramo de Mogotocoro, 3,700 m, *Killip & Smith 17647* (GH, NY, US); Alto del Almorzadero, 3,840 m, 6°59'N, 72°39'W, *St. John 20802* (GH, MICH, NY, RSA, S, UC, US). TOLIMA: 41 km E de Manizales, 3,250 m, *Forero et al. 3662* (COL, MO); Quindío Highway, W of Cajamarca, 3,200 m, *Killip & Varela 34554* (BM, COL, GH, S, US); Páramo de Ruiz, 3,400 m, *Pennell 3070* (GH, NY, US). VALLE: Hoya del Río Tuluá, entre Las Vegas y La Ribera, 3,300 m, *Cuatrecasas 20430* (F, RSA); Río Cali, Pichinde, 1,700 m, *Duque-Jaramillo 4183* (COL).

COSTA RICA, CARTAGO-SAN JOSÉ: Cerro de la Muerte, ca. 5 km above Villa Mills, 3,400 m, *Allen & Dodge 5680* (F, G, US), *Holm & Iltis 469* (A, F, G, UPS), *Whitmore 39* (F, MO, NY); La Asunción, 32 km N of San Isidro del General, 3,335 m, 9°34'N, 83°45'W, *Burger & Stolze 5989* (F), *Wilbur 21237* (DUKE); 8 km S of Taja, *Tessene 1474* (WIS); Cerro Buena Vista, *Weaver 1413* (DUKE).

ECUADOR, AZUAY: Nudo de Portete, 2,700 m, *Camp E-2169* (NY); Lago Zurru Cuchu, 3,700 m, *Prescott 829* (NY); Nabón, 3°20'S, 79°04'W, *Rose 23016* (US). BOLÍVAR: Western slopes of Volcán Chimborazo, 3,600 m, *Harling et al. 9632* (GB, MO, RSA); Simiatug, Hacienda Talahua, 3,200 m, *Penland & Summers 628* (F, GH). CAÑAR: El Tambo, 69 km S of Sibambe, 3,000 m, *Camp E-3982* (G, GH, MO, NY, P, RSA, UC, US); Cerro Buerán, 5 km S of Cañar, 3,600 m, *Fosberg & Giler 22639* (NY, US). CARCHI: Valle de Maldonado, 53 km W of Tulcán, 3,100 m, 0°50'N, 78°03'W, *Holm-Nielsen et al. 5570* (AAU, F, MO, NY, S, U); Páramo El Angel, 3,500 m, 0°41'N, 77°54'W, *Holm-Nielsen et al. 5289* (AAU, COL, F, MO, NY, S, U). CHIMBORAZO: Guamote, 3,000 m, *Asplund 6878* (CAS, G, S, UPS, US); Between Chunchi and Sibambe, 2,200 m, *Fagerlind & Wibom 783* (S); Páramo de Tililac, 3,600 m, *Harling et al. 6573* (GB, RSA); 14 km S of Mocha, 3,800 m, 1°29'S, 78°43'W, *Iltis E-481* (MO, WIS). COTOPAXI: 29 km E of Salcedo on Salcedo-Napo road, 3,860 m, *Boeke 778* (MO, NY); Pilalo-Latacunga road, 3,400 m, *Holm-Nielsen & Jeppesen 1477* (AAU, C, DS, NY, S); Volcán Cotopaxi, Hacienda Yacu-Tambo, 3,659 m, *Ugent & Alborno 5672* (DS, MSC, UC, US, WIS). IMBABURA: Lago Cuicocha, Islote Chica, 3,080 m, *Asplund 7161* (S); Río San Marcos, E of Volcán de Cayambe, 3,350 m, *Drew E-183* (C, COL, RSA, US); Mojanda, 10 km SSW of Otavalo, 2,900 m, 0°10'N, 78°18'W, *Sparre 13463* (S). LOJA: Loja, Angelica, 2,300 m, *Espinosa 363* (RSA); Lado sur de Saraguro, 2,300 m, *Espinosa 1386* (POM); Near Yangana, 2,000 m, *Hart 1032* (MO). MORONA-SANTIAGO: Entre Gualaceo y General Plaza, Km 29, 3,000 m, *Sparre 18777* (S). NAPO: Km 216 on Quito-Papallacta road, 3,700 m, *Berry 2522* (MO); Cerro Antisana, 4,000 m, 0°30'S, 78°00'W, *Grubb et al. 575* (DS, MSC, NY); 10 km E of Papallacta, 2,800 m, 0°21'S, 78°01'W, *Holm-Nielsen et al. 6839* (AAU, MO, NY, S). PICHINCHA: Tumbaco, 2,450 m, *Asplund 6554* (S); Pichincha, 3,650 m, *Asplund 6581* (S); Valle de La Magdalena, Chillogallo, 2,800 m, *Firmin 99* (F, S, US); Quito, *Humboldt & Bonpland in 1801* (F, P, RJ); Volcán Pichincha, *Sodirol in 1871* (BP, JE); Lagunita Linda, 3 km W of Paso de Guamaní, 3,900 m, *Sparre 15063* (S); W of Mt. Iliniza, 3,320 m, *Weydahl 153* (S). TUNGURAHUA: Patate, Hacienda Leito, 2,900 m, *Asplund 7961* (S); 10 km S of Mocha, 3,500 m, *Harling 6938* (GB); Vicinity of Ambato, Ficoa, *Pachano 145* (GH, NY, US); Río Colorado, Volcán Chimborazo, 4,200 m, *Sparre 18364* (S). ZAMORA CHINCHIPE: 20 km E of Loja on road to Zamora, 2,350 m, *Mathias & Taylor 5195* (RSA).

PERÚ, AMAZONAS: Chachapoyas, 6°13'S, 77°51'W, *Matthews in 1834* (BM, BR, E, K, OXF); Prov. Bongará, hills WNW of Pomacocha, 2,700 m, 5°50'S, 77°55'W, *Wurdack 924* (F, NY, RSA, UC, US). ANCASH: Cordillera Negra, Callán, 4,200 m, *Bernardi 16676* (G); Prov. Bolognesi, Parietana, E of Chiquián, 3,420 m, 10°09'S, 77°11'W, *Ferreira 5659* (MO, US, USM); Prov. Carazi, Laguna Parón, 4,100 m, 9°10'S, 77°35'W, *Mostacero et al. 547* (MO, NY). APURIMAC: Prov. Abancay, 16 km E of Abancay on Cuzco road, 3,000 m, *Iltis & Ugent 641* (DS, WIS); Prov. Andahuaylas, Mollebamba, 3,650 m, *Vargas 8721* (LIL). AREQUIPA: 20 km W of Arequipa, *Averett 1004* (MO); S slopes of Nevado Chachani, *Hinkley 65* (CAS, GH, NY, US); Prov. Cailloma, 15 km NE of Chivay, *Mueller et al. 2221* (LZ); Arequipa, Río Chili, 2,500 m, *Munz 15511* (F, GH, NY, POM); Pichu-Pichu, 3,000 m, 16°29'S, 71°15'W, *Sandeman 3758* (K, OXF); Prov. Condesuyos, Chuquibamba, 3,350 m, *Stafford 1165* (BM, F, K). AYACUCHO: Prov. Huanta, mountains NE of Huanta, 3,200 m, *Weberbauer 7505*

(F, GH, NY, US, WIS). CAJAMARCA: Prov. Contumazá, Lledén, 2,600 m, *Sagástegui et al.* 9408 (MO); Prov. Cajamarca, Granja Porcón (SIPA), 28 km NW of Cajamarca, 3,260 m, *Ugent* 5454 (DS, UC, WIS). CUZCO: Prov. Quispicanchis, Marcapata, 3,000 m, 13°30'S, 70°55'W, *Berry & Aronson* 3020 (MO); Sicuani, 3,551 m, *Hicken in 1903* (BAF, SI); Pampa de Anta, 7 km W of Anta, Ancahuasi, 3,150 m, *Iltis & Ugent* 783 (DS, MSC, UC, WIS); Cordillera Vilcabamba, Río Raccachaca, 4,500 m, *McSweeney in 1976* (MO); Ollantaitambo, *Munz* 15544 (NY, POM, US, WTU), *Pennell* 13670 (F, GH, NY, PH, S, US); La Raya, 4,400 m, *Pennell* 13514 (F, PH); Entre Paucartambo y Tres Cruces, Cerro de Cusilluyoc, 3,400 m, *Pennell* 14157 (F, GH, PH); Ausangate, 4,700 m, *Rauh-Hirsch* P1151 (RSA); 4 km NE of Cuzco on road to Pisac, 3,500 m, *Ugent* 4098 (DS, GH, MICH, MSC, UC, US, WIS); Prov. Paucartambo, 5 km NE of Paucartambo, 2,900 m, *Ugent & Vargas* 4407 (DS, US, WIS); Prov. Espinar, Huailapacheta, 14°45'S, 71°25'W, *Vargas* 6507 (CAS, LIL); Prov. Cañas San Andres de Checca, 3,860 m, 14°25'S, 71°20'W, *Vargas* 11014 (F, NA, UC); Prov. Urubamba, Cañón Chicón, 2,900 m, *Vargas* 11054 (F, GH, NA, UC). HUANCANELICA: San José de Acobambilla, 3,700 m, 12°40'S, 75°22'W, *Lloyd et al.* 536 (K); Prov. Tayacaja, Pampas, 3,250 m, *Stork & Horton* 10236 (F, G, GH, NA, UC); Prov. Huancavelica, Machajhuay between Conaica and Tinyajlla, 3,800 m, *Tovar* 801 (MO). HUANUCO: 9 km from Chirlín, 3,660 m, *Gentry et al.* 19214 (MO); Tambo de Vaca, 3,900 m, 9°42'S, 75°47'W, *MacBride* 4373 (F, GH, S, US); Pillao, 2,700 m, 9°40'S, 75°58'W, *Woytkowski* 34119 (F, GH, MO, UC). JUNÍN: Oroya, 3,700 m, *Kalenborn* 19 (DS, GH, MO, US). Prov. Yauli, Lago Huacracocha, 3,750 m, 11°40'S, 76°10'W, *López & Riccio* 10820 (RSA); Tarma, Hacienda Maco, 3,600 m, *Ochoa* 238 (CORD, NY). LA LIBERTAD: 70 km E of Trujillo, between Pampa and Yamobamba, 3,050 m, *Conrad* 2715 (MO); Entre Motil y Quiruvilca, Km 104–105, 3,300 m, *Ferreira* 3026 (MO, USM); Prov. Patate, entre Huancaspata y Tayabamba, 3,800 m, *López & Sagástegui* 8262 (MO). LIMA: Prov. Yauyos, Huancracha, 3,300 m, *Cerrate* 1180 (MO, USM); Río Blanco, 3,000 m, *Killip & Smith* 21579 (F, NY, S, US); *MacBride & Featherstone* 677 (F, GH, K, S, US); Prov. Huarochiri, Casapalca, 4,700 m, *MacBride & Featherstone* 857 (F, GH, S, US). MOQUEGUA: Saylapa, near Carumas, 3,300 m, 16°49'S, 70°43'W, *Weberbauer* 7337 (F, S). PASCO: La Quinua, 3,600 m, 10°33'S, 76°10'W, *MacBride & Featherstone* 2023 (F, GH, S, US); Paucartambo, 2,800 m, *Woytkowski* 6711 (GH); Cerro de Pasco, 4,130 m, *Ellenberg* 411 (MO). PUNO: Amantani, 3,900 m, 15°32'S, 70°01'W, *Aguilar* 234 (MO, USM); Prov. Azángaro, Cala-Cala, 4,100 m, 15°14'S, 70°33'W, *Bernardi* 16745 (G); between Ollachea and Macusani, *Dillon et al.* 1266 (MO); Prov. Sandia, 2–6 km S of Limbani, 3,550 m, *Metcalf* 30452 (UC, US); Santa Rosa, 80 km SSW of Ilave, 4,300 m, *Pearson* 33 (PH); Araranca, 4,100 m, *Pennell* 13432 (F, GH, NY, PH, S, US); Prov. Huancané, Occa Pampa, 3,965 m, 15°10'S, 69°35'W, *Shepard* 78 (GH, NY, US); 16 km NE of Macusani, 4,600 m, *Webster* 2 (K). SAN MARTÍN: Prov. Huallaga, valley of Río Apisoncho, 30 km above Jucusbamba, 2,800 m, 7°55'S, 77°10'W, *Hamilton & Holligan* 1411 (S, UC).

VENEZUELA, LARA: Las Sabanetas, above Los Aposentos, 2,530 m, *Steyermark* 55311 (F, MO, NY, VEN). MÉRIDA: La Carbonera, 2,200 m, *Aristeguieta* 2478 (F, MER, NY, US, VEN); Pico El Aguila, Carretera Chachopo, 3,600 m, *Badillo* 5176 (MY); Páramo de Los Conejos, 3,500 m, *Bernardi* 1257 (MER, NY); Páramo de Mucuchies, 3,750 m, *Humbert* 26304 (P, RSA, US); Laguna Mucubaji, 3,650 m, *Steyermark* 57508 (F). TÁCHIRA: Cabeceras del Río Quinimarí, 15 km S de San Vicente de La Revancha, 2,400 m, *Steyermark et al.* 100637 (VEN); Quebrada Agua Azul, 14 km SE de Delicias, 2,300 m, 7°31'N, 72°24'W, *Steyermark & Liesner* 118373 (MO, VEN). TRUJILLO: Near Guirigay, 3,300 m, *Aristeguieta & Medina* 3647 (NY, VEN); Dist. Boconó, Páramo de Tuñame, 3,120 m, *Berry* 3122 (MO); Entre La Peña y Agua del Obispo, 28–34 km de Carache, 2,400 m, *Steyermark* 104954 (M, S, VEN). ZULIA: Dist. Perijá, Serranía de Los Motilones, 10°00'N, 72°58'W, *Tillett & Honig* 747-834 (MO); Dist. Maracaibo, Serranía de Valledupar, 3,100 m, 10°25'N, 72°52'W, *Tillett* 747-1132 (MO).

Epilobium denticulatum is a common, widespread, highly variable species that has its primary distribution throughout the northern and central Andes. It may be distinguished from other closely related species by its nodding inflorescence, bluish or lavender staminal filaments, leaves with relatively few denticulate teeth, and strongly appressed, or more rarely, slightly spreading, minute blunt-tipped hairs on the surfaces of the leaf blades. This latter feature and colored staminal filaments are shared with *E. pedicellare*, but they are unknown in any other species. *Epilobium pedicellare* is immediately separable, however, by its alternate serrate leaves and erect inflorescences.

There are two other sympatric species, *E. fragile* and *E. ciliatum*, with which some plants of *E. denticulatum* might be confused. *Epilobium fragile* differs in its densely caespitose habit, thin wiry stems mostly less than 10 cm tall, sparse

pubescence, and few flowers. Some plants of *E. denticulatum* approach *E. fragile* in stature, but they generally have larger leaves, denser pubescence, more flowers and the appressed hairs mentioned above. *Epilobium ciliatum* is sympatric in a very limited area at the southern end of the range of *E. denticulatum*, and can be separated immediately by its white flowers, fleshy turions, and longitudinally ridged seeds.

Epilobium denticulatum was the first species described from South America. Its original circumscription and distribution, however, were based on two species, as recognized here, *E. denticulatum* and *E. puberulum*. From the beginning, the name *E. denticulatum* was used for the widespread northern Andean species. Specimens of *E. puberulum* have often been misidentified as *E. denticulatum*. These two species are allopatric, and, while they may be closely related, *E. puberulum* differs significantly in its erect inflorescences, complete lack of glandular hairs, distinct floral morphology, and petal color.

The long persistent confusion concerning the assignment of plants to the various taxa surrounding *Epilobium denticulatum* is well illustrated by the problems encountered by Haussknecht (1884). He recognized seven species in his group Denticulatae, one of which is a synonym of *E. pedicellare*. A careful reexamination of the specimens he used showed that five of the remaining six species are heterogeneous, containing components from two or more species. Thus, his treatments of *E. denticulatum*, *E. meridense*, and *E. caesium* include collections of *E. puberulum* (e.g., Coronel, Arauco Prov., Ochsenius, GOET; Hacienda San Juan, Valdivia Prov., Ochsenius, BREM; and Quebrada Verde, Valparaíso Prov., Maximow in 1854, JE, respectively), while *E. bonplandianum* included specimens of *E. ciliatum* from Mexico and South America (e.g., Cordillera Hurtado, Limarí Prov., Chile, Gay in 1837, P). Part of the confusion with this last name is probably due to the fact that the five specimens of *E. denticulatum* cited, including type material of *E. bonplandianum*, are all late season, flowered-out plants that are superficially very similar to some specimens of *E. ciliatum*. *Epilobium repens* was described from specimens from Volcán Orizaba, Mexico, that are referable to *E. ciliatum* (Hoch, 1978). Haussknecht, however, included four collections of *E. denticulatum* in the specimens cited under that species. Superficially, the Mexican specimens are similar to those of *E. denticulatum* from South America in stature, loose innovations, and the nodding inflorescences, but are distinguishable by other features. Although Haussknecht was a very astute observer of epilobiums and had a broad understanding of them on a world wide basis, the species that he included in his Denticulatae were apparently very troublesome to him. His *Monographie* (Haussknecht, 1884) formed the source for the report of *E. denticulatum*, *E. bonplandianum*, *E. caesium*, and *E. meridense* in the *Flora de Chile* (Reiche, 1898).

The most recent treatment, and the only subsequent work of any consequence, for *Epilobium denticulatum* is that of Samuelsson (1923). He recognized ten species and five varieties in this complex, of which six species and four varieties were proposed as new. Many of his new taxa were based on unique morphological types, which because of the relatively few collections available to him seemed amply distinct, e.g., *E. hirtum*, *E. bolivianum*. It is interesting to note that even though Samuelsson described a large number of new taxa, he discussed in several

places the difficulty of separating the species and their polymorphic nature (Samuelsson, 1923; p. 251, 255, 257). In a later publication (Samuelsson, 1930), he rejected two of these new species, *E. andicolum* and *E. asplundii*, considering them to be robust variants of *E. denticulatum*, and synonymized *E. denticulatum* var. *aberans* with *E. meridense* var. *helodes*. In delimiting most of his taxa, Samuelsson placed great emphasis on the density and distribution of pubescence, especially on the ovaries, pedicel length, and flower size, all of which are relatively variable characters.

Patterns of morphological variation within *E. denticulatum*, as circumscribed here, are extremely reticulate and diverse, and reflect the variety of selection pressures encountered throughout its enormous range. The same types of morphological features appear numerous times throughout its range, with some geographic differentiation. Superimposed on these patterns is variation because of elevational and microclimatic conditions, as well as interpopulational differences related to the high degree of autogamy and consequent fixation of certain characters.

The size, habit and branching patterns of *E. denticulatum* are extremely variable and are strongly influenced by exposure or elevation. The smallest plants are often found at higher elevations or in open or drier sorts of places. At these same elevations, however, much more robust plants can usually be found in more sheltered areas. There is also a pattern of increasing size at lower elevations. Most plants that exceed 80 cm in height come from areas below 3,000 m. Branching patterns are dependent on elevation and microclimate, but also on the age of the plants. Often stems are simple or with a few branches. As the plant ages, they may branch profusely or not at all. This feature is highly variable within populations and shows no geographic correlation. Many times, older stems that have nearly completed flowering may lose the nodding aspect of the inflorescence and appear erect.

Leaf size and, to a lesser extent, shape vary considerably and usually in parallel with the size of the plants, the smaller leaves on small plants, and larger ones on large plants. There are sporadic collections of extremely small-leaved plants from a number of different localities.

Similarly, large-leaved, usually more robust plants are also found throughout the range of the species with increasing frequency in southern Peru, Bolivia, and Argentina (e.g., Between Trujillo and Boconó, Edo. Trujillo, Venezuela, *Alston* 6503, BM; Entre Las Vegas y La Ribera, Dpto. Valle, Colombia, *Cuatrecasas* 20430, F, RSA; Chihuata, Dpto. Arequipa, Perú, *López & Miranda* 5530, RSA; Near La Cumbre, Dpto. La Paz, Bolivia, *Solomon* 5013, MO; Infiernillo, Tucumán Prov., Argentina, *Hjerting et al.* 9457, C). Plants of this type formed the basis for the names *E. andicolum* and *E. asplundii*.

Plants with very large leaves (greater than 5 cm) are found only in the altiplano and again in the Sierra Grande de Córdoba. Throughout the altiplano and southward in San Juan and Mendoza provinces, Argentina, there is a mixture of small and large-leaved plants, often within the same population. The populations from the Sierra Grande de Córdoba consist of predominantly large-leaved and usually robust plants. This pattern is modally different from that found in the rest of the range of *E. denticulatum* but is most likely the result of the derivation of the

Sierra Grande populations from more or less large-leaved plants from the southern altiplano to the west and northwest by long-distance dispersal.

The primary leaf shape in *E. denticulatum* is lanceolate, with acute apices. Rarely individuals may have nearly ovate leaves with subcordate bases (e.g., La Cumbre, Dpto. La Paz, Bolivia, *Asplund 4014*, the type of *E. bolivianum*; Nevado del Ruiz, Dpto. Caldas-Tolima, Colombia, *Barclay & Juajibioy 6380*, RSA; Calca, Dpto. Cuzco, Perú, *Hammerlund 620*, S). More frequently the larger-leaved plants mentioned above have somewhat elongate apices, so that the leaves are markedly acuminate.

Pubescence density and distribution is also extremely variable. In general, the upper stems and ovaries are strigillose with an admixture of appressed or slightly spreading glandular or blunt-tipped hairs. These hairs also occur on the surfaces of the leaves, a feature shared only with *E. pedicellare*. Often the leaves become glabrate as they mature, so that only a few or none of the appressed hairs are found on the surfaces of older leaves. Density of both hair types is highly variable throughout the range of the species, although there is a trend toward denser, almost canescent, strigillose pubescence in the southern páramos and altiplano. The increased pubescence may in part be due to the drier atmospheric conditions found throughout much of the altiplano, in contrast to the moist páramos found in Costa Rica, Venezuela, and Colombia, where this pubescence type is not common.

The most striking qualitative difference in pubescence type seen in *E. denticulatum* is the erect or spreading hirsute hairs that characterize plants that have gone under the name *E. hirtum* (e.g., Pichupichu, Dpto. Arequipa, Perú, *Sandeman 3758*; Chuquibamba, Dpto. Arequipa, Perú, *Stafford 1165*; La Paz, Bolivia, *Buchtien 531*; Socoroma, Tarapacá Prov., Chile, *Ricardi et al. 190*). The distribution of this character is limited to the vicinity of La Paz, Bolivia, Arequipa, Perú, and a single collection from Tarapacá Prov., Chile. In addition to the transformation of strigillose hairs to longer erect ones, the usually appressed glandular hairs of the leaves, stems, and ovaries are also erect and longer than normal.

Epilobium hirtum was originally described from robust, fairly large-leaved plants from La Paz, Bolivia. Except for pubescence, most of these plants are indistinguishable from those called *E. andicolum* (e.g., Ollantaitambo, Dpto. Cuzco, Perú, *Pennell 13670*). Mixed populations of plants with appressed and erect pubescence are indistinguishable except on the basis of the hair type (e.g., Río Chili, Arequipa, Dpto. Arequipa, Perú, *Munz 15511*). The hirsute pubescence gives the plants such a distinctive appearance that those with this feature are immediately identified as *E. hirtum*. This is an excellent example of the artificial separation of plants into different taxa based on a single character in a highly polymorphic group.

Flowers in *E. denticulatum* vary considerably in size, but exhibit no geographic patterns in their size distribution. Plants with very large flowers or very small ones are found throughout the range of the species, although the majority have petals of intermediate size. Even within populations flower size can be variable, with mixtures of large and small flowered plants (e.g., La Oroya, Dpto. Junín, Perú, *Kalenborn 19*; and Araranca, Dpto. Puno, Perú, *Pennell 13432*).

At anthesis most flowers, as well as the inflorescence, as a whole nod. In smaller flowers the anthers of the longer stamens, and often the shorter, usually

dehisce directly on the stigma, sometimes even before the flower fully opens. In larger flowers, the stamens are normally held away from the stigma at anthesis. After several hours, the longest bend inward, shedding their pollen on the stigma. Only rarely is the stigma completely exerted (Valle Paucartambo, Dpto. Cuzco, Perú, Herrera 3358, F); more frequently in the larger flowers, the stigma is partially exerted, but the longest stamens are able to reach at least the lower portion of the stigma, so some measure of self-pollination can take place (e.g., Ollantaytambo, Dpto. Cuzco, Perú, Pennell 13670, PH, GH, F, NY; Huanta, Dpto. Ayacucho, Perú, Weberbauer 7505, F, GH, NY, US). On cloudy or rainy days even the largest flowers may open only partially, or not at all, making them functionally cleistogamous.

Epilobium denticulatum is sympatric with at least *E. pedicellare*, *E. hirtigerum*, *E. glaucum*, and *E. ciliatum*, and presumably also with *E. fragile*. The geographic ranges of both *E. pedicellare* and *E. fragile* are completely contained within that of *E. denticulatum*. *Epilobium denticulatum* is sympatric with *E. hirtigerum* only in the Sierra Grande de Córdoba and with *E. ciliatum* in this same mountain range, and also in the Sierra de San Luis and in a narrow band in southern San Juan and eastern Mendoza Province, Argentina. *Epilobium glaucum* overlaps with *E. denticulatum* only in this last named area.

Natural hybridization involving *E. denticulatum* and any of these other species is apparently relatively rare. Several hybrids have been reported involving *E. pedicellare* (Samuelsson, 1923, 1930), but it is believed that all except one were based on non-hybrid specimens of *E. pedicellare* (q.v. for discussion), although hybrids of this combination would be very difficult to distinguish. Two specimens of what are possibly hybrids between *E. denticulatum* and *E. ciliatum* have been seen (Copina, Sierra Grande, Córdoba Prov., Argentina, Grassi 2280, LIL; and in the vicinity of Mendoza, Mendoza Prov., Argentina, Carrette in 1906, BA). Both have intermediate leaf shape, appressed hairs on the leaf surfaces, strongly reduced seed set, and pollen stainability of 27% and 23% respectively. Although *E. denticulatum* and *E. ciliatum* both have the same chromosome arrangement, AA, the depressed pollen stainability is not unusual. Artificial hybrids between these species had pollen stainability in the range of 37–65%.

The relationship of *E. fragile* with *E. denticulatum* is not clear (see discussion of *E. fragile*). There are several collections from northern Argentina and Chile (Río Despensas, Dpto. Humahuaca, Jujuy Prov., Argentina, Ruthsatz IV-60, MO; Río Despensas, Dpto. Cochimoca, Jujuy Prov., Argentina, Boelcke et al. 770, BAA; Km 99, camino Arica-Chapiquiña, Tarapacá Prov., Chile, Marticorena et al. 59, MO, CONC; Camino de Huara a Cancosa, al interior de Coscaya, Tarapacá Prov., Chile, Richardi et al. 418, MO, CONC) that approach *E. fragile*. They are tentatively retained in *E. denticulatum* because of their larger size, dense strigillose pubescence, and appressed hairs on the leaf surfaces. These plants will deserve careful reconsideration when more material becomes available from these poorly explored regions.

2. ***Epilobium pedicellare*** Presl, Reliquiae Haenkeanae 2:30. 1831. TYPE: "Chile," without specific locality, 1790, T. Haenke (PR-495768, holotype, photograph MO). Probably collected in Perú, and the label information is in error.

E. haenkeanum Hausskn., Oesterr. Bot. Z. 29:118. 1879. TYPE: Perú, without specific locality, 1790,

T. Haenke (PR, holotype, photograph MO, fragment JE). Hausskn., Monogr. *Epilobium* 268, tab. 16, f. 72, 72a. 1884. H. Lév., Iconogr. *Epilobium*, tab. 208. 1911. Samuelsson, Svensk Bot. Tidskr. 17:262. 1923. MacBride, Field Mus. Nat. Hist., Bot. Ser. 8(4):532. 1941.

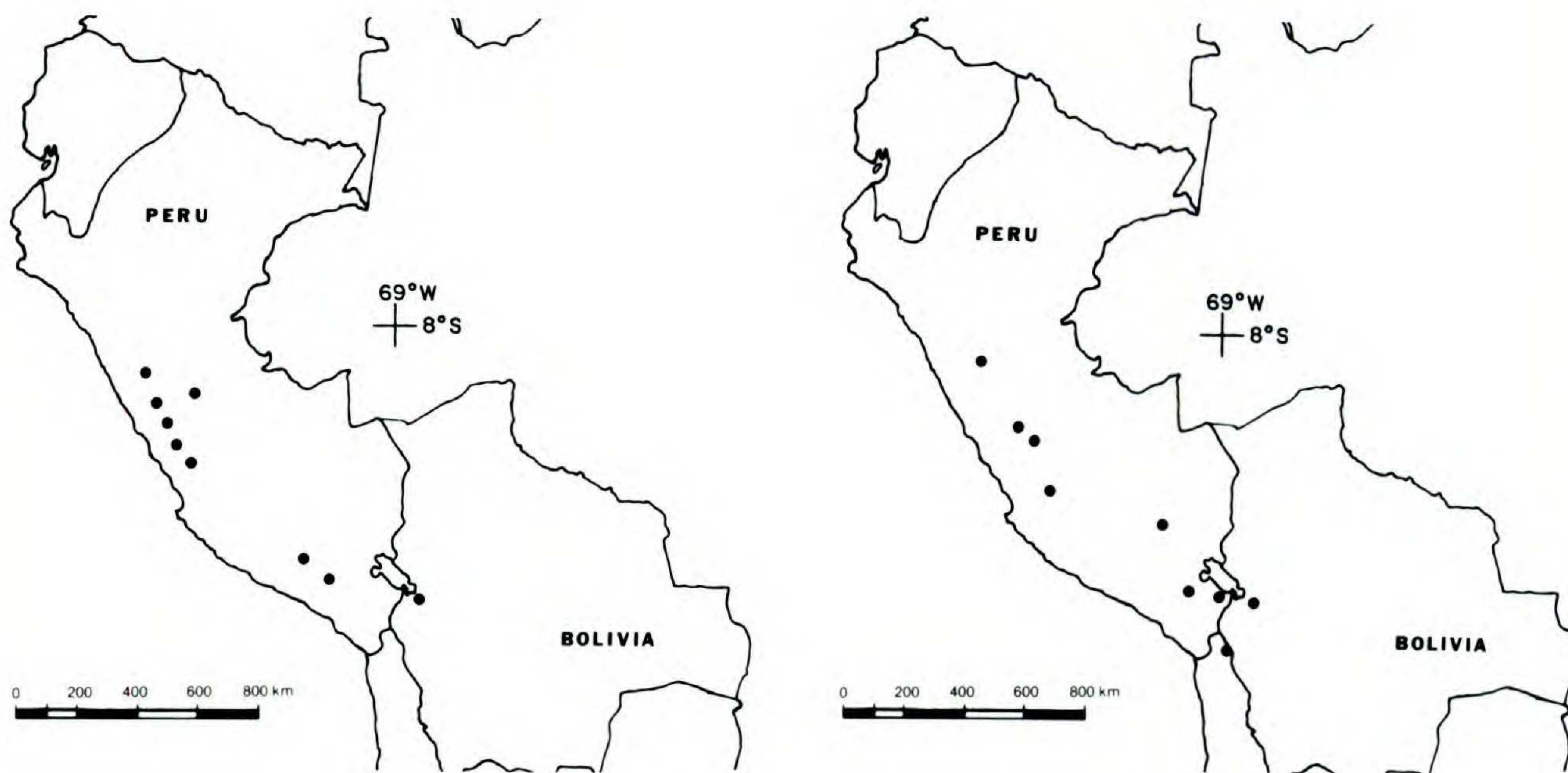
E. peruvianum Hausskn., Monogr. *Epilobium* 263. 884. TYPE: Perú, Dpto. Lima, "ditches and Río Rimac, near Lima," W. Nation (K, holotype, photograph MO). H. Lév., Iconogr. *Epilobium*, tab. 210. 1911.

Robust perennial herb, the stems (30–)40–120 cm long, reproducing vegetatively by elongate leafy shoots from near the base. Stems decumbent to pendent, or ascendent, sparsely branched above, usually with an abrupt bend leading to the erect inflorescence, thick, hollow, lustrous reddish brown, strigillose all around the stem in the inflorescence, below pubescence restricted to raised descending lines from the decurrent petiole bases. Leaves mostly alternate, opposite only on young shoots or near the base, thin, dark green, narrowly ovate to ovate, 1.2–4.3(–5) cm long, 0.5–1.4(–1.8) cm wide, acute to acuminate, rarely obtuse at the apex, finely serrate or doubly serrate with (7–)16–30(–43) irregularly sized teeth on each side, acute to cuneate at the base, sparsely strigillose on the margins and the abaxial midrib, both surfaces with appressed blunt-tipped or glandular hairs, 0.05–0.1 mm long, lateral veins prominent beneath, 3–4(–5) on each side of the midrib, on petioles 1–3(–4) mm long, rarely sessile. Inflorescence erect, simple, the flowers congested at anthesis, the internodes elongating somewhat in fruit. Flowers erect. Ovaries often reddish, strigillose, sometimes densely so, usually with scattered appressed glandular hairs, 0.7–1.5 cm long, on pedicels 0–1 mm long. Floral tube often reddish purple, 1.1–1.5 mm deep, 1.7–2.4 mm across, externally strigillose with scattered appressed glandular hairs, internally glabrous or with a few erect villous hairs, 0.1–0.15 mm long, in a ring near the base. Sepals often reddish purple, lanceolate, 2.5–3.4 mm long, 1.0–1.3 mm wide, strigillose with scattered appressed glandular hairs. Petals pale pink to rose purple, obovate, 3.5–5.5 mm long, 1.7–2.5 mm wide, the notch 0.9–1.3 mm deep. Anthers cream, 0.6–0.9 mm long, 0.4–0.6 mm wide; filaments bluish purple to pale lavender, those of the longer stamens 1.7–2.6 mm long, those of the shorter 0.7–1.8 mm long, the longer, and often the shorter, stamens shedding directly on the stigma at anthesis. Style white, 2.4–3.1 mm long; stigma white, clavate, 1.0–1.4 mm long, 0.6–0.8 mm thick. Capsules erect, with scattered strigillose hairs, 3.1–4.8 cm long, 1.1–1.5 mm thick, on pedicels 0.3–1.5(–2.5) cm long. Seeds brown, papillose, obovoid, 0.8–1.0 mm long, 0.3–0.4 mm thick, the chalazal end with a short appendage 0.04–0.08 mm long, 0.08–0.12 mm wide; coma white, 4.5–7 mm long, readily detaching. Gametic chromosome number, $n = 18$.

Distribution (Fig. 2): On moist stream embankments or seeps, widely scattered in the altiplano of central and southern Perú and western Bolivia at elevations of 2,400–3,600 m. Flowering throughout the year, but perhaps with reduced flowering from June through August, the coolest, driest months.

Specimens examined: BOLIVIA, LA PAZ: Prov. Murillo, La Paz, *Asplund* 58 (UPS); *Bang* 75a (NY, PH, US); *Buchtien* in 1907 (C, F, US), in 1910 (BAF, E, F, GB, GH, JE, L, NY, UPS, Z), in 1910 (BM), in 1912 (K), in 1913 (C, JE, LD, MO, S, UPS), in 1921 (GH), 8431 (US), 8433 (B, BM, BR, C, E, G, K, M, MO, S); *Pennell* 14217 (F, GH, NY, PH); *Rusby* 1806 (April 1885) (NY, WIS), 1806 (Oct. 1885) (F, GH, MICH, NY, PH, US); *Shepard* 157 (CAS, GH, NY, P); *Solomon* 5147 (MO); *Thuegsegges & Feurer* 4098 (MO); *Weddell* in 1851 (JE, P).

PERÚ, Without locality, *MacLean* (K); *Neé* in 1790 (F, MA). ANCASH: Prov. Cajatambo, Ocros, 3,400 m, 10°24'S, 77°24'W, *Weberbauer* 2706 (G, UPS). AREQUIPA: Arequipa, Río Chili, *Averett* 1007B



FIGURES 2-3.—2. Distribution of *Epilobium pedicellare*.—3. Distribution of *Epilobium fragile*.

(MO); Harvard Observatory, *Castle in 1911* (GH); without locality, *Harrison in 1896* (GH); Prov. Cailloma, Chivay, 3,500 m, 15°38'S, 71°36'W, *Mueller et al. 2134* (LZ). HUANUCO: Tambo de Vaca, 9°42'S, 75°47'W, *Martinet 168* (P). JUNÍN: Abocongo, *Infantes 160* (LIL). LIMA: Prov. Huarochirí, Viso, 2,700 m, *Asplund 11137* (S); Prov. Yauyos, Tupe, 2,950 m, 12°40'S, 75°46'W, *Cerrate 1116* (MO); Prov. Huarochirí, Picoy arriba de Surco, 3,200 m, 11°52'S, 76°28'W, *Ferreyra 6086* (MO, US, USM); Prov. Canta, entre Huascoy y Cormo, 3,000 m, 11°25'S, 76°45'W, *Ferreyra 18405* (MO); Matucana, *MacBride & Featherstone 90* (F, G, GH, S, US); *Martinet* (P); Río Chillón, Km 123 on road Canta-Culluhuay, *Mueller et al.* (LZ); Río Chillón, Obrajillo, 11°54'S, 77°09'W, *Pennell 14384* (PH); Río Huaura, 11°06'S, 77°39'W, *Ruiz & Pavón in 1778* (P).

Epilobium pedicellare is easily distinguished from the other South American species by its mostly alternate, finely serrate leaves, the teeth of uneven size, thick hollow stems, and an erect, congested inflorescence at least in early flowering. Only *E. hirtigerum* from eastern South America and the introduced *E. paniculatum* have mostly alternate leaves, but their ranges are widely separated from that of *E. pedicellare*, which is confined to the altiplano of Perú and Bolivia.

Presl originally described this species from a specimen collected by T. Haenke during the Malaspina Expedition (1789–1793). The herbarium sheet at Prague (PR) is labeled as coming from Chile, although this species is not known to grow within Chile as it was constituted in 1790, nor did Haenke collect in northern Chile, the only areas where *E. pedicellare* might be found (Kühnel, 1960). Undoubtedly the plant is mislabeled and probably came from Perú, since the many collections from the Malaspina Expedition are notorious for their incorrect labels (cf. Hitchcock, 1909).

Shortly after the appearance of *Reliquiae Haenkeanae*, Hooker & Arnott (1833) used the name *Epilobium pedicellare* to which they referred several Chilean and Argentinean collections of John Gillies. These proved to be a mixture of *E. denticulatum*, *E. ciliatum*, and *E. glaucum*, thus obscuring the identity of *E. pedicellare* early on.

The next botanist who dealt with any material referable to *E. pedicellare* was Haussknecht, who described *E. haenkeanum*, also from a Haenke specimen at

Prague (PR), but not the same one used by Presl (Haussknecht, 1879). Apparently Haussknecht never saw the type of *E. pedicellare*, although his annotations are found on a number of other specimens from Presl's herbarium. As a result, in the preparation of his *Monographie*, Haussknecht was uncertain as to the exact identity of *E. pedicellare* and tentatively assigned it as a synonym of *E. denticulatum* (Haussknecht, 1884).

To confuse the issue further, the type of *Epilobium haenkeanum*, at the time Haussknecht described it, was annotated as *E. denticulatum* with reference to Presl's brief description of that species in *Reliquiae Haenkeanae* (Presl, 1831). This description, however, differs substantially from the characters exhibited by the specimen. Haussknecht (1884) pointed out this discrepancy and provisionally placed Presl's description of *E. denticulatum* with his *E. caesium* without having seen the specimen from which Presl drew the description. Among the extant specimens at Prague (PR), there is a single sheet annotated as *E. denticulatum* in the same hand as the label for *E. pedicellare*, presumably that of Presl. This specimen is a small piece of a probable hybrid between *E. ciliatum* and *E. glaucum*, which matches the description of *E. denticulatum* as given by Presl and is probably the one on which it was based. Unfortunately, this specimen is labeled as coming from Chile, not Perú, as given in *Reliquiae Haenkeanae*, so some doubt still remains.

In his *Monographie*, Haussknecht (1884) also described a third taxon referable to *Epilobium pedicellare* as *E. peruvianum*, which he allied with *E. franciscanum* Barbey (*E. ciliatum* subsp. *watsonii* (Barbey) Hoch & Raven) to which it bears a vague resemblance but is not directly related.

As a result of Haussknecht's interpretation of *E. pedicellare* and the difficult access to Presl's material, subsequent authors have used the name *E. haenkeanum*, with *E. pedicellare* considered as a synonym of *E. denticulatum*.

Epilobium pedicellare has been relatively rarely collected and is apparently much more scattered in its distribution than the widespread *E. denticulatum* with which it often grows. This may be due to some ecological specialization because the only habitats where this species has been seen are very steep, almost vertical seeps that are continuously wet. In contrast, *E. denticulatum* is much more weedy, growing in ditches, seeps, stream banks, or almost any habitat that has a permanent supply of water. In places where *E. pedicellare* is found, it often grows in a pendent or reclining fashion with an abrupt U-shaped bend before the beginning of the erect inflorescence. The stems are often more than 1 m long and form dense masses. This unusual habit can often be seen on herbarium material and is very different from the ascending or erect stems and nodding inflorescences of *E. denticulatum*.

The nearest relative of *E. pedicellare* is probably *E. denticulatum*, with which it shares two unique characters, unknown in any other South American species: the presence of minute appressed or slightly spreading blunt-tipped hairs, usually on both surfaces of the leaves, and pale lavender to bluish staminal filaments.

Because the range of *Epilobium pedicellare* is completely contained in that of *E. denticulatum* and they often grow together, it would seem likely that hybrids would occasionally be produced. Samuelsson (1923, 1930) reported a number of plants as hybrids, but only one specimen of these seems likely to be of truly

hybrid origin (La Paz, Dpto. La Paz, Bolivia, *Buchtien* 37, US, mixed with *E. pedicellare*). The others fall within the variation seen in *E. pedicellare*, although hybrids of this combination are very difficult to distinguish. Based on the morphology of the two putative parents, the specimen indicated above is intermediate with leaves having fewer, less sharp teeth, thinner stems, and larger flowers than is typical for *E. pedicellare*. This specimen had a pollen stainability of 81%.

3. ***Epilobium fragile*** Samuelsson, Svensk Bot. Tidskr. 17:291, *tab.* 4, *f.* 3a–c. 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Murillo, “in rupibus irrigatis,” La Cumbre, 4,500 m, 26 May 1921, *E. Asplund* 4015 (UPS, lectotype, photograph MO; B (destroyed, photographs BH, MO, US), LD, S, W, Z, isoelectotypes). Samuelsson, Svensk Bot. Tidskr. 24:7. 1930. MacBride, Field Mus. Nat. Hist., Bot. Ser. 8(4):531. 1941.

E. nivale auct. non Meyen: Samuelsson, Svensk Bot. Tidskr. 17:290. 1923, pro parte; MacBride, Field Mus. Nat. Hist., Bot. Ser. 8(4):532. 1941.

Low, densely caespitose perennial herb, 3–10(–15) cm tall. Stems many, thin, usually reddish brown, decumbent or erect, mostly simple or few-branched from a fibrous, or somewhat woody rootstock, subglabrous, with a few strigillose hairs, 0.1–0.2 mm long, at the petiole bases, or occasionally scattered in descending lines from the petiole bases, rarely with a few erect glandular hairs, 0.1–0.2 mm long. Leaves all opposite or alternate in the inflorescence, thick, occasionally reddish purple, narrowly ovate to elliptic, rarely lanceolate, 0.4–1.2 cm long, 1.5–4 mm wide, obtuse to rounded, rarely acute at the apex, subentire with 0–3 obscure teeth on each side, acute to cuneate at the base, glabrous, or with a few scattered strigillose hairs on the margins, lateral veins obscure, none or 1–2 on each side of the midrib, on poorly defined petioles, 0–2.5 mm long. Inflorescence erect, simple, few-flowered. Flowers erect at anthesis. Ovaries reddish purple, 0.4–1 cm long, glabrous, or with a few strigillose or erect glandular hairs, on pedicels 1–9 mm long. Floral tube often reddish purple, 0.8–1.2 mm deep, 1.1–2.4 mm across, externally glabrous or with a few strigillose or erect glandular hairs, internally with a sparse ring of a few erect villous hairs, 0.08–0.13 mm long, near the base. Sepals often reddish purple, lanceolate, 2.5–3.3 mm long, 1.1–1.4 mm wide, glabrous. Petals pink to white, obovate, 3.0–5.5 mm long, 1.9–3 mm wide, the notch 0.4–1 mm deep. Anthers 0.6–0.8 mm long, 0.5–0.7 mm wide; filaments of the longer stamens 1.2–3 mm long, those of the shorter 0.7–2 mm long, at least the longer, and usually the shorter, shedding directly on the stigma. Style 1.7–2.6 mm long; stigma subcapitate, 0.8–1.2 mm long, 0.5–1.1 mm thick. Capsules erect, glabrous, 1.8–2.3 cm long, 1.1–1.5 mm thick, on pedicels 2–5 mm long. Seeds pale brown, minutely papillose, obovoid, 1.2–1.3 mm long, 0.4–0.5 mm thick, the chalazal appendage 0.04–0.08 mm long, 0.08–0.12 mm wide; coma pale yellow brown, 3.5–5 mm long.

Distribution (Fig. 3): Typically inhabiting moist crevices in rock outcrops or cliff faces; scattered throughout the Altiplano of Perú, from Dpto. Ancash south to western Bolivia and extreme northeastern Chile at elevations of 4,400–5,000 m. Flowering specimens have been collected from May, June, July and November.

Specimens examined: BOLIVIA, LA PAZ: Ravín de Chuquiaguillo, *Weddell in 1851* (P).

CHILE, I REGIÓN (TARAPACÁ): Parinacota, Lago Cotacotani, 4,500 m, 18°12'S, 69°15'W, *Sudzuki 480* (K).

PERU, ANCASH: Huaraz, 4,600 m, *Weberbauer 2969* (G). CUZCO: Ausangate, 4,800 m, *Rauh-Hirsch P1258* (RSA). HUANCANELICA: San José de Acobambilla, Nahuincocha, 12°40'S, 75°22'W, *Lloyd & Marshall 100* (K). JUNÍN: La Oroya, 35 km W of Hacienda Cochas, 5,000 m, *Gutte 3256* (LZ); Casa Cancha, Cerro La Viuda, 4,400 m, 11°05'S, 76°35'W, *Wilkes (U.S. Exploring Expedition in 1839)* (GH, K, US). LIMA: Prov. Huarochiri, Casapalca, 4,700 m, *MacBride & Featherstone 867* (F, GH, S, US). PUNO: Caccachara, 80 km SW of Ilave, 4,900 m, *Pearson 107* (PH); San Antonio de Esquilache, 4,500 m, 16°06'S, 70°18'W, *Stafford 729* (BM, F), *Tutin 1181* (BM).

Epilobium fragile is a diminutive, high Andean species that has been collected rarely, so little is known of its biology or relationships. It forms low, densely caespitose clumps, with the thin, wiry stems seldom more than 10 cm long. Plants are characteristically glabrous, except for a few strigillose hairs on the leaf margins, at the junction of the fused petiole bases, and rarely in scattered, descending lines, with or without a few scattered erect glandular hairs.

Epilobium fragile has usually been confused with *E. nivale*, even by Samuelsson, who described the former (Samuelsson, 1923). As a result, *E. nivale* has been erroneously reported from Peru (MacBride, 1941, and Samuelsson, 1923). Samuelsson considered *E. fragile* to be most closely related to *E. nivale*, both of which he segregated in his group Nivalia, based on their compact growth form, small leaves, and the more or less glabrous nature of the plants (Samuelsson, 1923). Superficially both species are quite similar in habit and overall morphology. However, *E. fragile* differs from *E. nivale* by the presence of strigillose and glandular hairs, thin, wiry stems, ovate to elliptic, blunt-tipped leaves, and slightly larger, often white flowers, although there is some overlap in all the characters except pubescence. Ecologically they are also separated, with *E. fragile* growing in crevices in rocks, and *E. nivale* inhabiting moist places near bogs or along streams. The present ranges of *E. fragile* and *E. nivale* are separated by about 1,500 km. Additional exploration of the Andes in northern Chile and northwestern Argentina, however, may expand the range of both species.

The chromosomal arrangement of *E. fragile* is unknown, so the possibility that it may be more closely related to *E. nivale*, which has the BB arrangement cannot be ruled out. A second, and what is considered more likely, hypothesis is that *E. fragile* is most closely allied to *E. denticulatum*, a species with the AA chromosomal arrangement, which is widespread in the northern and central Andes. In addition to having strigillose and glandular hairs in common, some of the smaller specimens of *E. denticulatum* approach *E. fragile* in habit, although they are larger, more densely pubescent, and usually have more and larger flowers. The geographic range of *E. fragile* is completely contained in that of *E. denticulatum*, and, considering the very recent nature of the high montane habitats where *E. fragile* is found, it may have been derived directly from *E. denticulatum*.

4. ***Epilobium puberulum*** Hook. & Arn., Hook. Bot. Misc. 3:309. 1833. TYPE: Chile, X Región (Los Lagos), Prov. Chiloé, Isla Chiloé, 1831, *H. Cuming 36* (K, lectotype here designated, photograph MO; BM, BP, BR (probable), E 2 sheets (photographs A, K), GH, OXF (probable), PRC, TCD, W (photographs BH, GH, MO), isoelectotypes). Hausskn., Monogr. *Epilobium* 257. 1884. Reiche, Fl. Chile 2:245. 1898. H. Lév., Iconogr. *Epilobium* tab. 192, 197 (as *E. bar-*

beyanum), 211 (as *E. denticulatum*). 1911. Samuelsson, Svensk Bot. Tidskr. 17:248. 1923.

E. denticulatum Ruiz & Pavón, Fl. Peruv. et Chil. 3:78. 1802, pro parte, as to plants from Concepción, Chile.

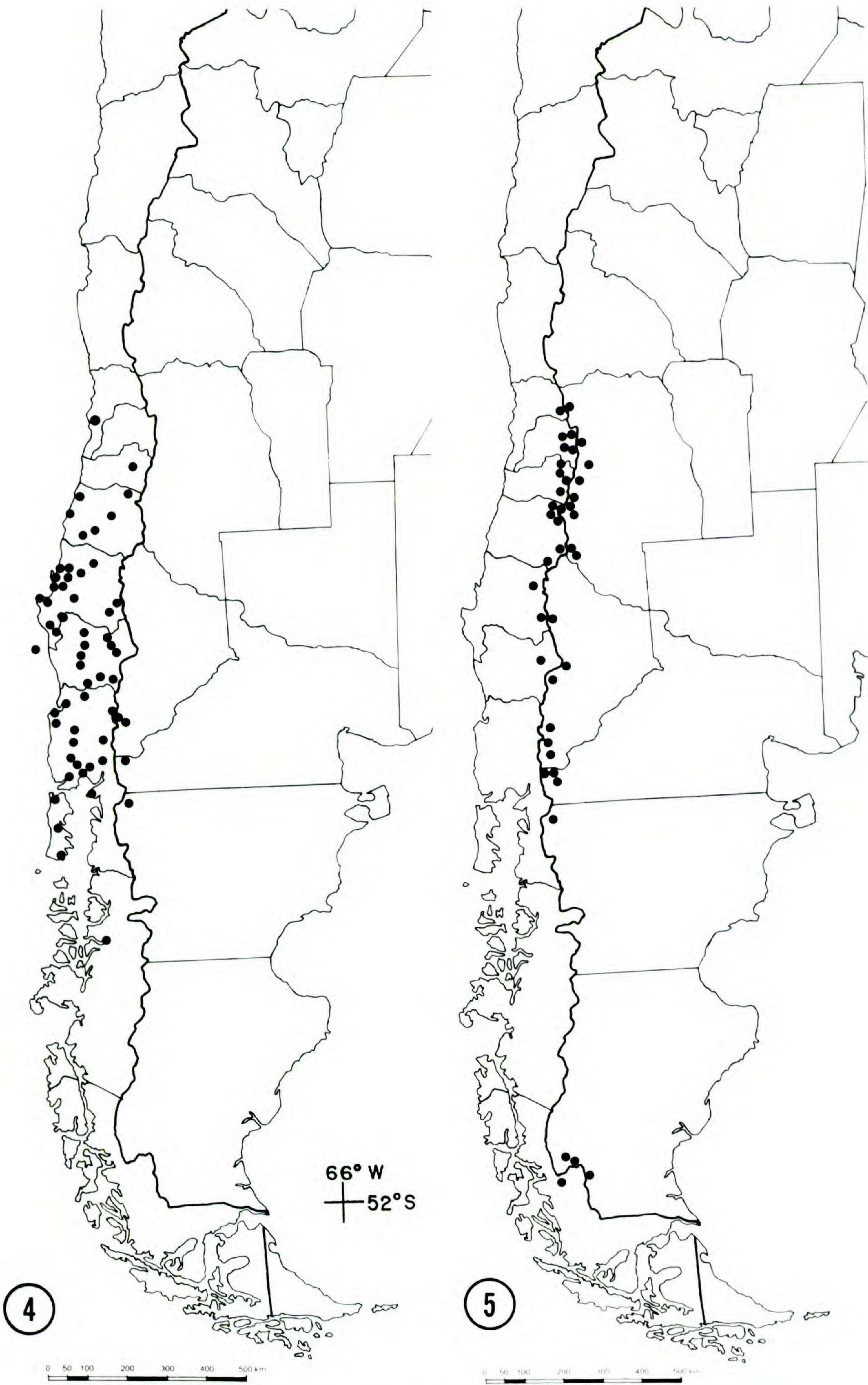
E. denticulatum auct. non Ruiz & Pavón: Gay, Hist. Fis. Chile 2:247. 1846.

E. pedunculatum R. Phil., Anal. Univ. Chile 41:713. 1872. TYPE: Chile, VI Región (O'Higgins), Cordillera de Colchagua, November 1860, C. Landbeck (SGO-53114, lectotype here designated, photograph MO; SGO-41459, isoelectotype, photographs GH, MO).

E. gracile R. Phil., Anal. Univ. Chile 84:748. 1893, non Bruegg., Jahres-B. Naturf. Ges. Graub. Ser. 2, 25:70. 1882. TYPE: Chile, X Región (Los Lagos), Prov. Valdivia, Cordillera de Valdivia, Pirihuaico, January 1887, O. Philippi (SGO-53083, lectotype here designated, photograph MO; SGO-53046, isoelectotype, photographs GH, MO).

Perennial herb, 20–60 cm tall, overwintering and reproducing vegetatively by elongate leafy shoots produced at or near the base. Stems erect, usually branched above, and often below, or simple, terete, strigillose to spreading hirsute throughout, the hairs 0.15–0.4 mm long, with obscure raised descending lines from the decurrent petiole bases, these often poorly developed or absent. Leaves mostly opposite, alternate above and in the inflorescence, often with fascicles of small leaves in the axils, thin, bright green, lanceolate to rarely narrowly ovate, 0.8–2.8(–3.3) cm long, 0.2–1(–1.5) cm wide, acuminate to acute at the apex, regularly and remotely denticulate with 3–6 teeth on each side, cuneate to acute, occasionally obtuse or rounded at the base, strigillose to spreading hirsute on both surfaces, usually glabrate with age and then the pubescence restricted to the margin and the abaxial and adaxial midribs and lateral veins, the lateral veins obscure, 2–4 on each side of the midrib, on more or less well defined petioles, 0.5–2 mm long. Inflorescence erect, simple or branched, the leaves subtending the flowers usually reduced in size. Flowers erect. Ovaries often reddish purple, densely strigillose to spreading hirsute, (0.8–)1.2–2.5(–3) cm long, on pedicels 0.4–1.3(–1.7) cm long. Floral tube 1–2 mm deep, 1.4–2.1 mm across, externally strigillose to spreading hirsute, internally with a ring of erect villous hairs, 0.2–0.3 mm long, near the base. Sepals lanceolate, 2–3.1 mm long, 0.9–1.3 mm wide, strigillose to spreading hirsute. Petals clear salmon pink, broadly obovate, 3.5–5 mm long, 2.5–3.2 mm wide, the notch 0.8–1.5 mm deep. Anthers cream to white, 0.6–0.8 mm long, 0.4–0.6 mm wide; filaments cream to white, those of the longer stamens 0.9–1.3 mm long, those of the shorter 0.3–0.6 mm long; only the longer shedding directly on the stigma at anthesis. Style cream to white, 2.1–2.8 mm long; stigma cream to white, clavate, 0.8–1.6 mm long, 0.5–0.8 mm thick. Capsules erect, strigillose or spreading hirsute, (2–)3.2–5(–6.6) cm long, 1–1.4 mm thick, on pedicels 0.5–2 cm long. Seeds brown, papillose, obovoid, 0.7–0.9 mm long, 0.3–0.4 mm thick, the chalazal end with a short appendage 0.04–0.08 mm long, 0.06–0.1 mm wide; coma white, 5–7 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 4): Frequent and somewhat weedy, along roadsides, gravelly or sandy stream beds, embankments, and other open, moist, usually disturbed sites. Widely distributed in central Chile from Valparaíso to Isla Chiloé, and Aisén (probably introduced at the latter). In Argentina, found only in a narrow band along the eastern slopes of the Andes in southern Neuquén, Río Negro, and northeastern Chubut provinces. Typically encountered from near sea level to 800 m, rarely as high as 1,000 m. Flowering October to March.



FIGURES 4-5. Distribution of *Epilobium* species.—4. *E. puberulum*.—5. *E. nivale*.

Representative specimens examined: ARGENTINA, CHUBUT: Cholila, *Crovetto* 3084 (SI). NEUQUÉN: San Martín de Los Andes, *Bridarolli* 2087 (LP); Hua-Hum, *Dawson & Schwabe* 2352 (BAB mixed with *E. ciliatum*); Lago Lácar, Peninsula Pucará, *Dawson & Schwabe* 2724 (BAA, BAB, MO). RÍO NEGRO: Bariloche, *Burkart* 6026 (RSA), *Maldonado in 1941* (F), *Parodi in 1934* (BAA, MO, S); Cerro Otto, 1,000 m, 41°09'S, 71°23'W, *Hosseus* 38 (BAF, CORD); Lago Nahuel Huapi, 770 m, *Ljungner* 158 (GB).

CHILE, V REGIÓN (ACONCAGUA): Valparaíso, Viña del Mar, Hacienda Las Siete Hermanas, *Bultmann* 23523 (CONC); Valparaíso, *Claude-Joseph* 3565 (US); Quebrada Verde near Valparaíso, *Maximow in 1854* (JE). VI REGIÓN (O'HIGGINS): Cachapoal, Termas de Cauquenes, *Gay* 187 (F, P, RJ; mixed with *E. ciliatum*); *Reid* (K mixed with *E. glaucum*). Colchagua, without locality, *Philippi* (JE, SGO). VII REGIÓN (MAULE): Curicó, Vichuquen, 34°53'S, 72°00'W, *Philippi* 627a (SGO); 5 km above Los Queñes, 760 m, 35°00'S, 70°45'W, *Solomon* 4335 (MO). Linares, Quinamávica, *Philippi in 1893* (SGO); Linares, *Quezada in 1975* (MO). Talca, Cordillera de Talca, El Picazo, *Barros* 82 (GH); Constitución, *Reiche in 1890* (SGO). VIII REGIÓN (BÍO-BÍO): Arauco, Contulmo, *Behn in 1919* (M); Lanahue, 37°56'S, 73°17'W, *Claude-Joseph* 5980 (US); Arauco, 50 m, *Pennell* 12966 (PH); Llico, *Philippi in 1861* (SGO); Boca del Río Tubul y Raqui, *Ricardi in 1949* (CONC); Isla Mocha, Laguna Hermosa, *Weldt-Rodríguez* 1166/461 (CONC). Bío-Bío, Camino de Bío-Bío a Santa Barbara, Estero Pirquinco, 400 m, 37°49'S, 71°40'W, *Martcorena et al.* 1015 (CONC, MO); Cordillera de Antuco, La Cueva, *Philippi in 1882* (G, SGO). Concepción, Tomé, Collén, *Junge in 1934* (CONC); Gualqui, *Kuntze in 1892* (NY); Florida, *Merxmüller* 24865 (M); Nonguén, near Concepción, *Moore* 296 (LA); Coronel, *Ochsenius in 1866* (BR, GOET); Concepción, *Dombey in 1782* (P), *Elliot* 148 (BM, E, NY), *Ruiz & Pavón in 1782* (MA). Ñuble, Entre Cabrero y Salto del Laja, Fundo Trilahue, 130 m, *Martcorena et al.* 855 (CONC); Cuchacucha, *Née in 1793* (MA); Montañas de Chillán, *Philippi* (SGO); Pilmaiquén, 36°40'S, 71°51'W, *Philippi* (G); Bulnes, *Philippi in 1878* (JE, SGO); 8 km E of San Rafael on road to San Ignacio, 36°35'S, 72°45'W, *Solomon* 4394 (MO). IX REGIÓN (ARAUCANÍA): Cautín, Laguna Lorilón, Fundo Flor, *Behn in 1946* (CONC); Villarrica, *Burger in 1965* (GOET); Freire, *Claude-Joseph* 5882 (US); Pemehue, 39°29'S, 72°30'W, *Germain in 1894* (SGO); Truf-Truf, 150 m, 38°44'S, 72°34'W, *Gunckel* 16908 (US); Pelún, 38°30'S, 72°20'W, *Lanfurgo in 1885* (SGO); 2 km S of Metrenco, *Moore* 310 (LA, MO); Termas de Palguín, 700 m, 39°22'S, 71°45'W, *Solomon* 4525 (MO). Malleco, Cordillera de Nahuelbuta, Los Alpes, Fundo Solano, *Eyerdam* 10296 (F, NY, SGO, UC, US); Curacautín, *Maldonado* 39 (L); Curacautín, Río Blanco, *Pennell* 12726 (F, GH, NY, PH, SGO); Pidima, Fundo Chequenco, 38°01'S, 72°26'W, *Pfister in 1946* (CONC); 16 km N of Curacautín, 800 m, 38°20'S, 70°50'W, *Solomon* 4489 (MO). X REGIÓN (LOS LAGOS): Chiloé, Puerto Carmen, Quellón, 43°08'S, 73°46'W, *Martcorena* 1766 (CONC); Camino de Caicumeo, *Philippi in 1886* (SGO); 14 km S of Castro, *Weldt-Rodríguez* 734-29 (CONC). Llanquihue, Colegual, 41°22'S, 73°11'W, *Klenner in 1952* (CONC); Hautrunes-Maullín, *Pfister* 289 (CONC); Lago Todos Los Santos, Petrohué, *Stubbe in 1961* (VALD); 5 km N of Puerto Montt, *Wall & Sparre in 1947* (S). Osorno, Cuinco, 40°32'S, 73°10'W, *Rudolph in 1933* (VALD); Chuyaca, *Rudolph in 1944* (VALD); 3 km E of Puyehue, 40°40'S, 72°18'W, *Solomon* 4596 (MO); Centinela, *Sparre* 4399 (S); Osorno, *Wall & Sparre in 1947* (S). Palena, Rolecha, 41°55'S, 72°50'W, *Pfister in 1951* (CONC). Valdivia, Valdivia, *Buchtien in 1901* (BAF, BM, BREM, E, M, P, S, US); *Lechler* 441 (G, GH, GOET, K), *Philippi* 514 (BM, BREM, G, GOET, JE, P, UPS); Panguipulli, *Claude-Joseph* 2556 (US); Corral, *Gunckel* 15424 (GH); 5 km NE of La Unión, *Moore* 297 (LA, MO); Hacienda San Juan, 40°15'S, 73°05'W, *Philippi in 1886* (JE, SGO); Cordillera de Ranco, Huahum, *Philippi in 1887* (SGO); Cordillera Pelada, *Philippi in 1889* (JE, SGO). XI REGIÓN (AISEN): Aisen, Aisen, *Andreas* 509 (U).

Epilobium puberulum is a distinctive species of south central Chile. Its densely strigillose stems and ovaries with generally small lanceolate, few-toothed leaves, erect habit, and salmon-pink flowers make it easily recognized from all its congeners. In fact, the flower color, unknown in any other species of *Epilobium*, is sufficient to identify living material immediately. Superficially some plants of *E. puberulum* have a strong resemblance to some individuals of *E. denticulatum*. There are, however, a number of striking morphological differences; in addition, these two species are allopatric, with a gap of several hundred kilometers between them at their closest point. *Epilobium puberulum* is much more strict in habit and lacks the glandular hairs and nodding inflorescence of *E. denticulatum*, and the flower color is distinctive.

The nearest relative of *E. puberulum* is probably *E. denticulatum*. *Epilobium*

puberulum may have the same chromosomal arrangement as *E. denticulatum* (AA), although this has not yet been confirmed.

The first collections of *E. puberulum* were made by Ruiz, Pavón, and Dombey, from the vicinity of Concepción, Chile, during their stay there in 1782 and 1783. Because of the similarity of these specimens to collections of *E. denticulatum* from Peru, they were all described under the name *E. denticulatum*. Not until some thirty years later were the Chilean plants recognized as a separate species. In subsequent years, R. A. Philippi published two additional taxa based on trivial variants.

Variation within this species is primarily in the size and density of the leaves and the branching pattern. These have no geographic basis, but are mostly related to the age of the plant and the season in which it was collected. Early season plants tend to be simple with fairly large leaves (mostly up to 2.5 cm), with fascicles of small leaves in their axils. As the growing season progresses, these axillary shoots may elongate, producing densely branched plants. The leaves of the secondary shoots are often smaller than those of the primary branches produced earlier. Pubescence also varies, not only in density but in type. For example, a collection from La Unión, Valdivia Prov., Chile (*Moore 297*, MO) is finely strigillose throughout with mostly glabrate leaves, while one from Vegas Blancas, Malleco Prov., Chile (*Solomon 4459*, MO) is densely spreading hirsute with both surfaces of the leaves pubescent.

Ecologically, *E. puberulum* is distinct from most other species. Although it does grow sympatrically with three species, its distribution is the inverse of the normal pattern. As was indicated earlier, except for *E. hirtigerum* and *E. puberulum*, all the South American species are montane, with a few descending to much lower altitudes at higher latitudes. In contrast, *E. puberulum* grows at lower elevations in the coast range, central valley, and the lower slopes of the Andes in Chile, seldom extending above 1,000 m. Its limited and scattered distribution in Argentina suggests that it is a relatively recent introduction to the eastern slopes of the Andes, perhaps appearing there only with the clearing of the forest land and increased communication across the Andes during the last century. The single collection from Aisén, Chile, is undoubtedly a recent introduction.

The high degree of enforced autogamy mentioned earlier makes hybridization with other species an extremely rare event. With one exception no evidence was seen in any of the populations examined in the field or from herbarium material that would indicate that hybridization takes place, although it is not an absolute impossibility. There is one set of very unusual collections made by Bridges at Valparaíso, Chile during the 1830s (*Bridges 179*, BM, E, K, W), apparently all from the same plant or population, which can only be explained as being of hybrid origin, with *Epilobium ciliatum* as the other likely parent. While the upper inflorescence is very *E. puberulum*-like, the lower leaves are several times longer and broader (4.5×2 cm), with many more teeth, than is known in any other collection of *E. puberulum*. The leaves approach a size and shape common for *E. ciliatum*, which also occurs in the same area. The flowers are borne singly in the axils of leaves throughout the length of the simple stems, with the antipetalous staminal filaments ca. 0.5 mm long, as is normal in *E. puberulum*. The average pollen stainability of these plants was 74% (range 67–88%). This unusual set of specimens was

identified by Haussknecht as belonging to *E. caesium*, the type of which came from northern Bolivia.

5. *Epilobium ciliatum* Raf., Med. Repos. II 5:361. 1808. subsp. **ciliatum**. TYPE: Northern Pennsylvania, *C. S. Rafinesque*. No specimens of this species collected by Rafinesque are known. (Only the synonymy for names based on South American material is given; for a complete discussion of North American names see Hoch, 1978.)

E. pedicellare auct. non Presl: Hook. & Arn., Bot. Misc. 3:309. 1833, pro parte.

E. pedicellare β *latifolium* Walp., Nov. Act. Acad. Caes. Leopold. 19, Suppl. 1:328. 1843. TYPE: Chile, VI Región (O'Higgins), Cordillera de San Fernando, *January–March 1831, F. Meyen* (B, holotype, destroyed). No other authentic material has been seen. Haussknecht places *E. pedicellare* β *latifolium* as a synonym of *E. chilense* and cites a collection of Meyen from the Cordillera de San Fernando at Berlin (B) (Haussknecht, 1884, p. 272). Based on this placement, the brief description and locality, this variety probably belongs here.

E. tetragonum auct. non L.: Hook. f., Fl. Antarct. 2:270. 1847, pro parte; Fl. N. Z. 1:60. 1853, pro parte, as to the plants from the Falkland Islands.

E. chilense Hausskn., Oesterr. Bot. Z. 29:118. 1879. TYPE: Chile, without specific locality or date (1826–31), *H. Cuming* (W, lectotype here designated, photograph MO; BM, BR, M, OXF, PR 2 sheets, isoelectotypes). Hausskn., Monogr. *Epilobium* 272. 1884. Reiche, Fl. Chile 2:249. 1898. H. Lév., Iconogr. *Epilobium*, tab. 168. 1911. Samuelsson, Svensk Bot. Tidskr. 17:269. 1923.

E. cunninghamii Hausskn., Oesterr. Bot. Z. 29:118. 1879. TYPE: Chile, XII Región (Magallanes), Prov. Magallanes, Punta Arenas (Sandy Point), 28 February 1863, *R. Cunningham* (LE, holotype, not seen; K, JE (probable), isotypes). Samuelsson, Svensk Bot. Tidskr. 17:276. 1923.

E. valdiviense Hausskn., Oesterr. Bot. Z. 29:118. 1879. *E. chilense* var. *valdiviense* (Hausskn.) Hoss., Trab. Inst. Bot. Farm., Buenos Aires 33:57. 1915. TYPE: Chile, X Región (Los Lagos), Valdivia, *R. A. Philippi* (W, holotype, photograph MO). Hausskn., Monogr. *Epilobium* 271. 1884. Reiche, Fl. Chile 2:249. 1893. H. Lév., Iconogr. *Epilobium*, tab. 166. 1911. Auct. non Hausskn.: Skottsberg, Kungl. Sv. Vet. Akademiens Handlingar 50(3):42. 1913. Samuelsson, Svensk Bot. Tidskr. 17:272. 1923.

E. bonplandianum auct. non H.B.K.: Hausskn., Monogr. *Epilobium* 267. 1889, pro parte as to the plants from Mexico and Chile. Reiche, Fl. Chile 2:246. 1898.

E. magellanicum R. Phil. & Hausskn. ex Hausskn., Monogr. *Epilobium* 271. 1884. TYPE: Chile, XII Región (Magallanes), Prov. Magallanes, without precise locality, summer 1864–65(?), *R. A. Philippi* (W, lectotype here designated, photograph MO; W, JE, SGO-41443, SGO-53016, W (last 4 probable), isoelectotypes). The date is taken from SGO-53016. Reiche, Fl. Chile 2:248. 1898. H. Lév., Iconogr. *Epilobium*, tab. 171. 1911. Samuelsson, Svensk Bot. Tidskr. 17:278. 1923; Svensk Bot. Tidskr. 24:9. 1930.

E. aconcaguinum R. Phil., Anal. Univ. Chile 84:745. 1893. TYPE: Chile, V Región (Aconcagua), Prov. Los Andes, Los Andes, on the banks of the Río Aconcagua, December 1885, *R. A. Philippi* (SGO-53036, lectotype here designated, photographs GH, MO; SGO-53010, isoelectotype).

E. albiflorum R. Phil., Anal. Univ. Chile 84:745. 1893. TYPE: Chile, X Región (Los Lagos), Prov. Valdivia, Hacienda San Juan, 40°15'S, 73°05'W, January 1886, *R. A. Philippi* (SGO-53044, lectotype here designated, photograph MO).

E. glandulosum auct. non Lehm. Reiche, Fl. Chile 2:250. 1898.

E. valdiviense var. *alboffii* Macloskie, Rep. Princeton Univ. Exped. Patagonia 8:611. 1905. TYPE: Argentina, Terr. Tierra del Fuego, Ushuaia, *N. Alboff*. No authentic material has been seen. This name was originally published without an indication of rank. The varietal level has been chosen because this was the generally used concept at the time of publication.

E. santa-cruzense Dusén, Kungl. Sv. Vet-Akad. Arkiv. f. Botanik 7(2):208, tab. 3, f. 2–4, tab. 7, f. 29–34. 1907. TYPE: Argentina, Prov. Santa Cruz, upper valley of the Río Santa Cruz, 11 February 1905, *P. Dusén* 5842 (S, lectotype here designated, photograph MO; K, SI, UPS, isoelectotypes). Samuelsson, Svensk Bot. Tidskr. 17:278. 1923.

E. hookerianum Hausskn. ex Skottsberg, Kungl. Sv. Vet. Akademiens Handlingar 56(5):271. 1916. TYPE: Falkland Islands, East Falkland, between Port Darwin and North Arm, 27 January 1908, *C. Skottsberg* 122 (UPS, lectotype here designated, photograph MO; BA, GB, LD, S, SGO, isoelectotypes).

E. chilense var. *latifolium* Samuelsson, Svensk Bot. Tidskr. 17:270. 1923. TYPE: Chile, V Región

- (Aconcagua), Valparaíso, *T. Bridges* (K, lectotype here designated, photograph MO; G, isolecotype). Based on *E. chilense* f. "latifolia" Hausskn., Monogr. *Epilobium* 272. 1884.
- E. chilense* var. *macrum* Samuelsson, Svensk Bot. Tidskr. 17:271. 1923. TYPE: Chile, V Región (Aconcagua), Prov. Quillota, Campana de Quillota, 1856–57, *Ph. Germain* (W, lectotype here designated, photograph MO; K, SGO-53057, SGO-53098, isolecotypes). Based on *E. chilense* f. "macra" Hausskn., Monogr. *Epilobium* 272. 1884.
- E. longipes* Samuelsson, Svensk Bot. Tidskr. 17:271, tab. 4, f. 2. 1923. TYPE: Argentina, Prov. Chubut, Lago Buenos Aires, mouth of Río Fenix, 11 December 1890, *C. Skottsberg* 946 (UPS, lectotype here designated, photographs MO, S).
- E. argentinum* Samuelsson, Svensk Bot. Tidskr. 17:273, tab. 3, f. 5. 1923. TYPE: Argentina, Prov. Mendoza, Río Salado Superior, Cajón de Las Aguas Amarillas, 22 January 1893, *F. Kurtz* 7621 (JE, lectotype here designated, photographs MO, S).
- E. constrictum* Samuelsson, Svensk Bot. Tidskr. 17:275, tab. 4, f. 4. 1923. TYPE: Argentina, Prov. Santa Cruz, Lago Argentino, Valle del Río Santa Cruz, 19 January 1905, *P. Dusén* 5614 (S, lectotype here designated, photographs MO, S; BAF, SI, UPS, isolecotypes).
- E. caesiovirens* Samuelsson, Svensk Bot. Tidskr. 17:279, tab. 4, f. 1. 1923. TYPE: Argentina, Prov. Mendoza, Las Cuevas, Puente del Inca, 2,700–2,800 m, 13 February 1903, *G. O. Malme* 2889 (S, lectotype here designated, photograph MO; B (destroyed, photographs BH, MO, US), S, UPS, W, isolecotypes).
- E. leiophyton* Samuelsson, Svensk Bot. Tidskr. 17:280, tab. 3, f. 1. 1923. TYPE: Chile, VII Región (Maule), Cordillera de Curicó, 2,500 m, January 1897, *C. Reiche* (UPS, lectotype here designated, photograph MO; B (destroyed, photographs BH, GH, MO, NY, US), isolecotype).

Variable perennial herbs (5–)20–60(–90) cm tall, overwintering and reproducing vegetatively by fleshy-leaved turions or compact leafy rosettes produced at or below ground level, the leaves of the perennating structures subentire, obovate to depressed obovate, or ovate to depressed ovate, 0.5–1.5 cm long, 0.5–2 cm wide. Stems erect, occasionally ascendent, often well branched from the base or above, or sometimes simple, terete or quadrangular, reddish brown or purplish above, strigillose, the hairs 0.1–0.2 mm long, throughout in the inflorescence, glabrate below, then strigillose in raised descending lines from the decurrent petiole bases, with an admixture of erect to slightly appressed glandular hairs, 0.1–0.2 mm long, mostly in the inflorescence, occasionally throughout, rarely glabrous. Leaves opposite, alternate above, thin, green, lanceolate to narrowly ovate (0.6–)1.3–6.5(–7.5) cm long, (0.3–)0.6–2.6(–3.1) cm wide, acuminate to acute at the apex, remotely, irregularly serrulate with (8–)10–22 teeth on each side, obtuse to rounded, subcordate or occasionally cordate at the base, glabrous or with a few scattered strigillose hairs on the margins, the lateral veins 4–5(–7) on each side of the midrib, on petioles 0–3 mm long. Inflorescence erect, often branched, rarely somewhat nodding, the leaves subtending the flowers much reduced, acuminate, and usually narrower. Flowers erect. Ovaries often reddish purple, strigillose, usually with an admixture of erect to appressed glandular hairs, (0.8–)1–2.2 cm long, on pedicels 2–5 mm long. Floral tube often reddish, 0.9–1.5 mm deep, (0.8–)1.2–2.2 mm across, externally strigillose, usually with an admixture of erect to appressed glandular hairs, internally usually with a ring of erect villous hairs, 0.1–0.2 mm long near the base, often with only a few hairs present and occasionally glabrous. Sepals often reddish, lanceolate, 1.8–2.8 mm long, 0.8–1.2 mm wide, strigillose, usually with an admixture of erect to appressed glandular hairs. Petals white, often flushed with pink after anthesis, or pink, obovate, 3.0–4.5 mm long, 1.5–2.5 mm wide, the notch 0.7–1.5 mm deep. Anthers cream to white, 0.5–0.7 mm long, 0.4–0.5 mm wide; filaments cream to white, those of the longer stamens 1.5–2.2 mm long, those of the shorter 0.8–1.5 mm

long; the longer, and usually the shorter, stamens shedding pollen directly on the stigma before or at anthesis. Style cream to white, 1–1.8(–2.3) mm long; stigma clavate to subcapitate (0.8–)1.5–2.5 mm long, 0.4–0.8 mm thick. Capsules erect, with scattered strigillose and glandular hairs, 3–6.2 cm long, 1–1.6 mm thick, on pedicels 0.4–1.5(–2.2) cm long. Seeds gray brown, narrowly obovoid, 0.9–1.4 mm long, 0.3–0.5 mm thick, with conspicuous longitudinal rows of flattened, fused papillae, at least along the sides, the micropylar end acuminate, the chalazal end with a short appendage, 0.04–0.08 mm long, 0.08–0.2 mm wide; coma white to slightly yellowish, 5–8 mm long, readily detaching. Gametic chromosome number, $n = 18$.

Distribution (Fig. 6): Common and weedy in open, often disturbed areas, usually permanently moist, or at least moist for part of the growing season, such as roadsides, sandy and gravelly stream beds, embankments, boggy areas, and banks of lakes and ponds. In South America, throughout the Andes of Chile and Argentina from central IV Región (Coquimbo), Chile, and San Juan Prov., Argentina, southward to Tierra del Fuego, in the coast range between Santiago and Valparaíso, generally throughout the central valley and coastal hills south of Concepción, scattered eastward on the Patagonian plain in southern Chubut and Santa Cruz Prov., Argentina, and in the Sierra de San Luis and Sierra Grande de Córdoba; also in the Falkland Islands. In North America from Alaska to British Columbia, eastward throughout much of Canada to Labrador, southward through New England to Pennsylvania and parts of the Appalachians, southwestward from Michigan and Indiana across the northern high plains to Colorado and New Mexico, throughout the mountains and basins of the western U.S. to the Pacific coast, south in Mexico along the Sonoran and Chihuahuan deserts to the mountains of southern Mexico and central Guatemala. Also in Japan, Korea, northeastern China, and eastern Siberia. Introduced in Hawaii, Europe and European U.S.S.R., New Zealand, and parts of Australia and Tasmania (Raven & Raven, 1976). In the northern part of its South American range found from 1,200–2,900 m, gradually descending to sea level on the western side of the Andes near Concepción. In the southern part of the range mostly between 200 and 1,900 m, and in Tierra del Fuego from sea level to 350 m. Flowering primarily from December to March throughout, but as early as September in the northernmost parts of the coastal mountains of Chile.

Representative specimens examined: ARGENTINA, CHUBUT: Colonia Sarmiento, *Birabén* 555 (LP); Dpto. Cushamén, 30–40 km NE of Esquel, 42°49'S, 71°05'W, *Boelcke et al.* 16036 (BAA, MO); Dpto. Futuleufú, Esquel, La Hoya, *Cabrera et al.* 25987 (LP); Lago Fontana, *Castellanos in* 1932 (BA, MO, RSA); Lago Futalaufquén, *Castellanos in* 1945 (F, LIL); Cholila, *Crovetto* 3009 (SI); Golondrinas, 42°01'S, 71°31'W, *Crovetto* 3197 (BAB, LIL); Valle de Las Plumas, Lago General Paz, *Gerling* 43 (BAF); 72 km S of Tecka, crossing Río Cherque, 800 m, *Hjerting* 629 (C); Valle del Lago Blanco, 45°54'S, 71°15'W, *Koslowsky* 172 (BA); Trevelin, Estancia Río Frío, *Krapovickas* 4000 (BAB); Lago Puelo, desembocadura del Epuén, *Pérez-Moreau in* 1940 (BA, LIL, RSA); Parque Nacional Los Alerces, Lago Cisnes, *Pérez-Moreau in* 1944 (BA); Lago Epuén, *Soriano* 1374 (BAA, SI); Río Senguer, Estancia Laurita, 44°43'S, 70°04'–24'W, *Soriano* 1480 (BAA, SI); Dpto. Tehuelches, Arroyo Temenhua, 44°13'S, 71°16'W, *Soriano* 2651 (BAB). CÓRDOBA: Dpto. San Alberto, Pampa de Achala, 2,000 m, *Cabrera et al.* 16620 (LP); Sierra Grande, cerca del Río Yuspe detrás del Cerro Blanco, 1,650 m, *Hunziker* 10253 (CORD, MO, RSA mixed with *E. hirtigerum*); Sierra Achala, Cerro de Los Gigantes, *Kurtz* 3879 (CORD, RSA); Sierra Grande, Cuesta de Copina, 1,610 m, 31°50'S, 64°10'W, *Solomon* 4149 (MO); Sierra Grande, La Cumbrecita, 1,450 m, 31°55'S, 64°15'W, *Solomon* 4199 (MO). MENDOZA: Dpto. Las Heras, puente del Inca, Laguna de Los Horcones, *Boelcke et al.* 9823 (BAA,

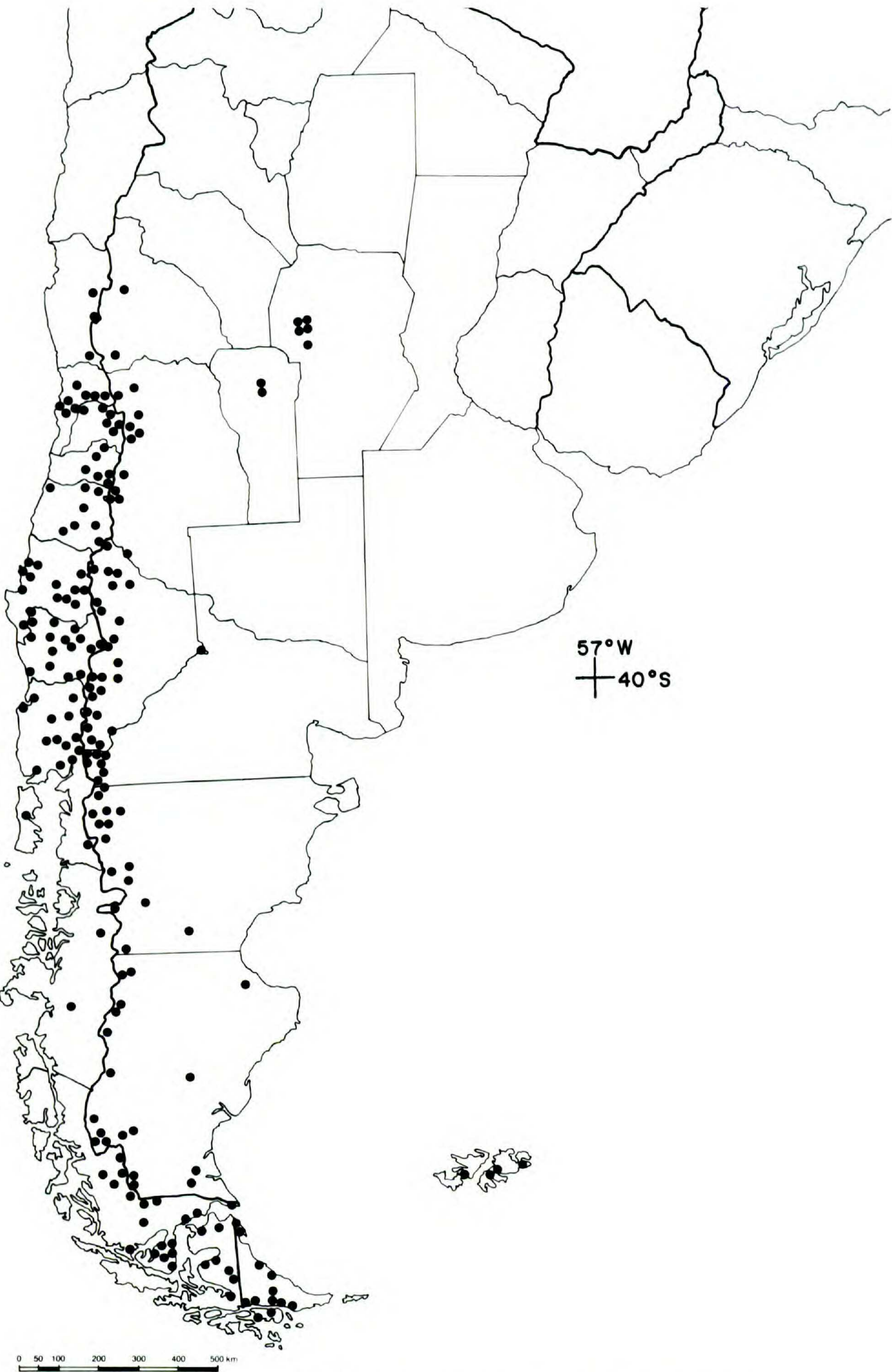


FIGURE 6. Distribution of *Epilobium ciliatum* ssp. *ciliatum* in South America.

BAB, MO). Dpto. Malargüe, Arroyo Las Mangas, 2,000 m, *Carette* 284 (LP, SI); Dpto. Malargüe, Arroyo del Cordón del Cura, *Castellanos in 1941* (BA, RSA); Dpto. San Carlos, Refugio Gral. Alvarado, 2,000 m, *Cuezzo & Barkley 20MZ451* (NY); Arroyo Chacayco, above Laguna Carilauquén, 36°32'S, 70°11'W, *Kurtz 6086* (JE); Río Salado Superior, Los Molles, *Kurtz 7550* (JE); Dpto. San Rafael, Río Atuel, entre Puesto de Ubilla y Paso del Pico Plateado, *Kurtz 7592* (CORD, JE, LP); Dpto. San Carlos, Arroyo de Yaucha, 33°46'S, 69°02'W, *Kurtz 11153* (CORD); Dpto. Tupungato, Finca Los Helechos, 33°20'S, 69°11'W, *Leal 1259* (LIL); Dpto. Tunuyan, Rincón Colorado, 2,800 m, *Leal 1289* (RSA); Dpto. Tupungato, Estancia La Carrera, 2,350 m, *Melis & Paci in 1949* (BR, G, W); Dpto. Las Heras, Uspallata, 2,000 m, *Semper 540* (LIL, NY); Valle del Atuel, Cajón del Burro, 2,400 m, *Wilczek 412* (G). NEUQUÉN: Lago Nahuel Huapi, Isla Victoria, 770 m, *Boelcke 1795* (BAA, SI); Dpto. Minas Las Ovejas, 37°01'S, 70°45'W, *Boelcke et al. 10752* (BAA, BAB, MO); Dpto. Minas, Laguna Epulauquén, 1,300 m, 36°50'S, 71°04'W, *Boelcke 10856a* (BAA, BAB, MO); Dpto. Chos Malal, Vegas del Pelán, 1,700 m, 36°54'S, 70°20'W, *Boelcke et al. 11140* (BAA, BAB, MO); Dpto. Minas, Varvarco Campos, Arroyo Benítez, 36°17'S, 70°39'W, *Boelcke et al. 14224½* (BAA, MO); confluencia de los Ríos Neuquén y Varvarco, Invernada Vieja, *Boelcke et al. 14439* (BAA, BAB); Arroyo Chacayco, 37°05'S, 69°45'W, *Chicchi 91* (LP); Río Limay, *Chicchi 193* (LP); Dpto. Huiliches, Volcán Lanín, Arroyo Rucu-leufú, *Correa et al. 5596* (BAB mixed with *E. australe*); Parque Nacional Lanín, Baños de Epulafquén, *Correa et al. 5843* (BAB); Pampa del Malleo, 39°48'S, 70°58'W, *Crovetto AN-128* (CTES); Rahue, Estancia Ochoa, 39°23'S, 70°49'W, *Dawson & Schwabe 2129* (BAA, BAB); Hua-Hum, *Dawson & Schwabe 2352* (BAA, BAB; mixed with *E. puberulum*); 10 km from Junín de Los Andes towards Zapala, 900 m, *Hjerting 6306* (C); Neuquén, *Jergensen 636* (BAB); Lago Lolog, *Kalela 1756* (H); Dpto. Ñorquín, Cajón de Trolope, 37°46'S, 71°04'W, *Kurtz 6184* (CORD, JE); Parque Nacional Lanín, San Martín de Los Andes, Cerro Chapelco, 1,700 m, *León & Calderon 978* (BAA); Cerro de Copahue, Fuente Zulena, *O'Donnell 2072* (LIL); Dpto. Los Lagos, Villa La Angostura, *Pedersen 1547* (BR, C, MO, P, US); Lago Nahuel Huapi, Península Quettrihue, *Pérez-Moreau in 1940* (BA, RSA); Dpto. Catán-Lil, Estancia Bernal, Arroyo del Cañadón, 39°34'S, 70°36'W, *Pérez-Moreau 3077* (BAB); Dpto. Chos-Malal, Canchahuiganco, 37°01'S, 70°23'W, *Ragonese 166* (BA, RSA); Dpto. Loncopué, Cajón Chenque Pehuén, 38°06'S, 70°55'W, *Rugolo & Agrasar 130* (BAA); Dpto. Catán-Lil, Cerro Chachil, 39°05'S, 70°38'W, *Rugolo & Agrasar 372* (BAA, MO); Lago Nahuel Huapi, Brazo Huemul, Arroyo Huelta, 40°58'S, 71°22'W, *Solomon 4623* (MO); Camino El Huecú a Loncopué, 1,000 m, *Spegazzini 175* (BAB); Dpto. Picunches, Pino Hachado, Arroyo Haichol, *Valla et al. 3009* (BAA, CTES, MO); Lago Quillén, *Valla et al. 3204* (BAA, CTES, MO). RÍO NEGRO: Parque Nacional Nahuel Huapi, Laguna Frías, 41°05'S, 71°50'W, *Boelcke & Correa 5379* (BAA, BAB, SI); Bariloche, 770 m, *Buchtien in 1905* (BAF, BP, BREM, E, F, GB, GH, JE, L, M, PR, S, SI, US, W, Z), *Cabrera 5942* (F, GH, LP, NY, POM, US); Parque Nacional Nahuel Huapi, Lago Fonck, *Pérez-Moreau in 1942* (BA, RSA); Cascada del Mallín Ahogado, El Bolsón, *Scolnik 318* (LIL); Cerro V. Lopéz, W of Bariloche, 1,000 m, 41°03'S, 71°35'W, *Solomon 4611* (MO); Villa Cerro Catedral, 1,030 m, 41°10'S, 71°28'W, *Solomon 4613* (MO); Río Llogdconto, 41°22'S, 71°30'W, *Solomon 4630* (MO); Cerro Tronador, 1,200 m, *Solomon 4637* (MO); 3.9 km S of Campamento La Veranada, 1,000 m, 41°28'S, 71°28'W, *Solomon 4642* (MO); Dpto. Pilcaniyeu, Pilcaniyeu, Estancia Raylluso, *Vallerini 424* (BAA). SAN JUAN: Dpto. Iglesia, El Rodeo, 30°12'S, 69°06'W, *Cuezzo 1848* (LIL); Dpto. Calingasta, Cordillera del Espinazito, Los Manantiales, 2,770 m, 32°14'S, 69°58'W, *Kurtz 9610* (BAF, CORD); Dpto. Calingasta, Las Lumbreras, 2,000 m, *Spegazzini 655* (BAB). SAN LUIS: Sierra de San Luis, Cerro Canutal, 32°46'S, 66°05'W, *Castellanos in 1929* (BA); Cerro Sololosta, 32°51'S, 66°00'W, *Pastore 84* (SI). SANTA CRUZ: Chonque-Aike, 49°16'S, 69°45'W, *Ameghino in 1898* (LP); Dpto. Lago Argentino, Estancia María Elisa, 50°20'S, 71°60'W, *Ancibor & Vizinis 4626a* (BAA, MO); Dpto. Río Chico, Lago Pueyrredón, Río Oro, 500 m, *Boelcke et al. 12897* (BAA, BAB); Dpto. Lago Buenos Aires, 29 km NW of Perito Moreno, 46°25'S, 71°09'W, *Boelcke et al. 16097* (BAB, MO); Camino a Paso Roballos, 47°11'S, 71°36'W, *Boelcke et al. 16176* (BAA, MO); Dpto. Lago Argentino, Lago San Martín, Estancia Cancha Rayada, 48°54'S, 72°26'W, *Boelcke et al. 16293* (BAB, MO); Tehuelches, 250 m, 46°50'S, 67°27'W, *Donat 283* (BM, CAS, F, G, GB, GH, K, MO, NY, S, SI, U, UC, Z); Cerro Buitreras, 51°43'S, 70°09'W, *Hauthal in 1899* (CORD); Between Cerro del Fraile and Cordón de Los Cristales, 50°32'S, 72°39'W, *James 471* (BM, DS, SI); Cerro Buenos Aires, 350 m, 50°24'S, 72°59'W, *James 3004* (BM); Río Coyle, Hotel Las Horquetas, 51°24'S, 70°17'W, *Rahn 4396* (C); Río Los Antiguos, 300 m, 46°32'S, 71°38'W, *Roivainen 2526* (H). El Calafate, 190 m, 50°20'S, 72°15'W, *Solomon 4653* (MO); Glaciar Perito Moreno, 190 m, 50°28'S, 73°02'W, *Solomon 4658* (MO); Lago Volcán, Estancia El Rincón, 47°46'S, 72°15'W, *Spegazzini 324* (BAB); Dpto. Güer Aike, Estancia Stag River, 51°34'S, 71°57'W, *T.B.P.A. (Boelcke et al.) 3280* (BAB, MO, RNG); Pto. Tres Marías, 700 m, 51°28'S, 72°05'W, *T.B.P.A. (Ambrosetti & Mendez) 3680* (MO); Lago Argentino, Brazo Onelli, 300 m, *Vervoorst 4560* (LIL, S, W). TIERRA DEL FUEGO: Río Grande, *Expedición Fac. de Ciencias E.F.y N. 140* (BA); Estancia Harberton, 30 m, *Goodall 71* (LP, RNG); Río Lashifashaj, Brown's sawmill on Ruta O, 40 m, *Goodall 585* (E, LP, MICH, NA, RNG, RSA, UC, US); Estancia Moat, *Goodall 641* (MICH, NA, RNG, SI, UC, US, WIS; mixed with *E. australe*); Estancia Viamonte, Estero Manantiales,

Goodall 906 (NA, RNG); Estancia Cullen, Río Cullen, *Goodall 3180* (LTR, NA); Estancia Cullen, Arroyo Beta, *Goodall 3224* (MICH, NA, RNG, UC); Lago Fagnano, *Hunziker 6711* (BAB, UC). Bahía Lapataia, *Pérez-Moreau in 1948* (BA, MO, RSA); 1 km NW of Ushuaia, 50 m, *Solomon 4712* (MO); Ushuaia, Arroyo Buena Esperanza, 150 m, *Solomon 4741* (MO).

CHILE, IV REGIÓN (COQUIMBO): *Choapa*, Cuncumén, 1,050 m, 31°55'S, 70°35'W, *Solomon 4273* (MO). *Limarí*, Cordillera de Hurtado, 30°30'S, 70°30'W, *Gay 523* (P); Río Gordito, 3,000 m, 31°02'S, 70°20'W, *Jiles 2548* (CONC). V REGIÓN (ACONCAGUA): Los Andes, 10 km W of Río Blanco, 32°55'S, 70°19'W, *Hutchison 131* (UC, US); Los Andes, *Philippi in 1882* (SGO). *Petorca*, Cerro Chache, 18 km E of La Ligua, 1,900 m, *Morrison 17050* (G, GH, K, MICH, MO, NA, UC, WTU). *Quillota*, Limache, Cajón Grande, *Boelcke 432* (BAA, SI). *San Felipe*, San Felipe, *Claude-Joseph 2488* (US). *Valparaíso*, Camino a Laguna Verde, 33°06'S, 71°41'W, *Behn in 1930* (CONC); Concón, *Garaventa 500* (BH, CONC); Cerro del Colliguay, 33°12'S, 71°07'W, *Jaffuel 656* (GH); Valle de Marga-Marga, *Jaffuel & Piri6n 3094* (GH). REGIÓN METROPOLITANA (SANTIAGO): *Cordillera*, Río Yeso, Laguna Los Piuquenes, 2,500 m, *Biese 808* (LIL, NY); El Volcán, 1,300 m, 33°50'S, 70°12'W, *Burkart 9346* (SI); San José de Maipo, 1,050 m, 33°40'S, 70°20'W, *Solomon 4313* (MO). *Melipilla*, Las Vizcachas, 10 km from La Dormida, 1,860 m, *Morrison 16779* (G, GH, MO, NA, S, SI, UC). *Santiago*, 5 km above Farellones, La Parva, 2,700 m, *Moore 397* (LA, MO); Maitenes, Pérez Caldera, 1,800 m, 33°11'S, 70°29'W, *Skottsberg & Sparre 11082* (CONC, S); Junction of road to La Disputada with road to Farellones, 1,400 m, 33°20'S, 70°20'W, *Solomon 4291* (MO). VI REGIÓN (O'HIGGINS): *Cachapoal*, Río Coya above El Teniente, 2,900 m, *Pennell 12307* (GH, PH, SGO); Baños de Cauquenes, *Pérez-Moreau in 1948* (BA, MO, RSA). *Colchagua*, San Fernando, *Bertero 237* (P); Termas Vegas Del Flaco, 1,750 m, *Mahu 9747* (H, MO, UC); Rincón de Tinguiririca, *Ricardi in 1950* (CONC, LIL); 19.3 km above La Rufina, 1,000 m, 34°55'S, 70°30'W, *Solomon 4330* (MO). VII REGIÓN (MAULE): *Curicó*, La Montaña, 34°54'S, 70°54'W, *Mahu 10756* (MO); Cordillera del Planchón, *Née in 1793* (MA, mixed with *E. glaucum*); 6.2 km above Los Queñes, 780 m, 35°00'S, 70°45'W, *Solomon 4332* (MO). *Linares*, Panimávida, 35°45'S, 71°25'W, *Philippi in 1883* (BM). Quinamávida, prope Parral, *Philippi in 1893* (JE, SGO); Cajón Troncoso, 36°20'S, 70°45'W, *Schlegel 3695* (CONC). *Talca*, Cordillera de Talca, El Picazo, *Barros 84* (GH); 52.4 km above El Colorado, 900 m, 35°50'S, 70°55'W, *Solomon 4338* (MO). VIII REGIÓN (BÍO-BÍO): *Arauco*, Laraquete, 37°10'S, 73°11'W, *Hosseus 85* (CORD); Contulmo, Lago Lanalhue, *Ricardi in 1949* (CONC, LP; mixed with *E. puberulum*). Bío-Bío, Entre Cabrero y Salto del Laja, 37°07'S, 72°23'W, *Martcorena et al. 852* (CONC, MO); Dpto. La Laja, Cuñibal Oriente, 150 m, 37°31'S, 72°15'W, *Martcorena et al. 874* (CONC, MO); Camino de Santa Barbara a Río Huequecura, Puente Piulo, 290 m, 37°42'S, 72°00'W, *Martcorena et al. 891* (CONC); Estero Epún, 1,260 m, 37°52'S, 71°28'W, *Martcorena et al. 970* (CONC, MO); On road to Laguna La Laja, 1,400 m, 37°25'S, 71°20'W, *Solomon 4434* (MO); Antuco, 530 m, 37°20'S, 71°40'W, *Solomon 4445* (MO). *Concepción*, Tomé, *Junge in 1935* (CONC); *Concepción*, *Junge 3016* (US); 5 km SW of Concepción, 200 m, *Skog 1030* (CONN); 9.7 km W of San Rafael, 450 m, 36°35'S, 72°45'W, *Solomon 4403* (MO). *Nuble*, Termas de Chillán, Garganta del Diablo, *Gleisner 162* (CONC, MO); Termas de Chillán, 1,720 m, *Moore 412* (LA, MO), 2,200 m, *Werdermann 1314* (E, K, NY, S, UC, US, Z; mixed with *E. australe*); 8.2 km E of San Rafael, 300 m, 36°35'S, 72°45'W, *Solomon 4395* (MO). IX REGIÓN (ARAUCANÍA): *Cautín*, Desembocadero del Río Toltén, 39°15'S, 73°14'W, *Friedrich in 1934* (CONC); 4 km SW of Termas de Palguín, 780 m, *Moore 302* (LA, MO); Temuco, banks of Río Cautín, *Roivainen 2994* (H); Puente Correntoso, 15 km E of Villarrica, 210 m, 39°16'S, 72°00'W, *Solomon 4536* (MO); Pitruquén, 100 m, 38°59'S, 72°39'W, *Sparre 3454* (S). *Malleco*, Cordillera de Nahuelbuta, Los Alpes, Fundo Solano, 590 m, *Eyerdam 10296* (NY); Parque Nacional de Nahuelbuta, Pino de Canales, *Mahu 5860* (MO); Arroyo Lumaco, Capitán Pastene, 100 m, 38°11'S, 73°00'W, *Martcorena et al. 1224* (CONC); Entre Pino Hachado y Liucura, 1,080 m, *Martcorena et al. 1434* (CONC); Dpto. Victoria, Termas de Tolguaca, 1,180 m, *Morrison & Wagenknecht 17500* (G, GH, MO, S, SI, UC); Curacautín, 700 m, *Pennell 12715* (F, GH, NY, PH, SGO); Buenavista below Volcán Tolguaca, 1,100 m, *Pennell 12815* (F, GH, NY, PH, SGO); Pidima, Fundo Chequenco, *Pfister in 1946* (CONC); Laguna San Pedro, Lonquimay, *Pinto in 1953* (CONC); 2.8 km below Vegas Blancas, 37°45'S, 72°58'W, *Solomon 4472* (MO); 30 km W of Curacautín, 500 m, 38°20'S, 72°05'W, *Solomon 4472* (MO); 30 km W of Curacautín, 500 m, 38°20'S, 72°05'W, *Solomon 4473* (MO); Termas del Río Blanco, 1,300 m, 38°35'S, 71°35'W, *Solomon 4496* (MO); Lago Icalma, 1,000 m, 38°48'S, 71°16'W, *Zöllner 7868* (MO). X REGIÓN (LOS LAGOS): *Chiloé*, Castro, *Gay 63* (P); Piruquina, *Junge 291* (CONC). *Llanquihue*, Paso Pérez Rosales, 980 m, *Moore 325* (LA); Camino Ensenada a Ralún, *Pfister in 1946* (CONC); Calbuco, *Philippi in 1893* (JE, SGO); Río Maullín, *Wall in 1947* (GB). *Osorno*, Salto Pilmaiquén, *Rudolph in 1931* (VALD); Chuyaca, 40°34'S, 73°07'W, *Rudolph in 1933* (VALD); Ñadi Caipulli, *Rudolph in 1951* (VALD); 7.7 km E of Puyehue, 200 m, 40°40'S, 72°18'W, *Solomon 4592* (MO); Lago Constanca, 1,000 m, *Sparre & Smith 353* (CONC, mixed with *E. australe*). *Palena*, Río Palena, *Delfin in 1887* (SGO). *Valdivia*, Cordillera de Ranco, without collector (844) in 1852 (GOET, JE); Corral, 30 m, *Gunckel 3195* (BH); Lago Puyehue, Isla Fresia, *Mahu in 1956* (MO); Camino de Coñaripe a Puerto Fui, Km 6, *Martcorena et al. 473* (CONC); San Juan, 40°15'S, 73°05'W, *Philippi in 1887* (SGO);

Valdivia, *Philippi in 1888* (CORD, K, US). XI REGIÓN (AISEN): *General Carrera*, Valle León, Lago Buenos Aires, 550 m, *von Rentzell 6242* (GH, SGO, SI); *Ventisquero Soler*, 500 m, 46°52'S, 73°08'W, *Seki 547* (CONC). *Coihaique*, Lago Seco, 45°35'S, 72°02'W, *Schlegel 2345* (CONC). XII REGIÓN (MAGALLANES): *Antártica Chilena*, Isla Navarino, 3 km W of Puerto Williams, 100 m, *Moore 353* (LA, MO); Isla Navarino, Puerto Douglas, 55°10'S, 68°08'W, *Vervoorst 385* (LIL). *Magallanes*, Morro Chico, 52°02'S, 71°26'W, *without collector or date* (WU); Seno Otway, Río El Canelo, *Biese 1249* (LIL); Río Tres Brazos, 10 m, 53°16'S, 71°02'W, *Cekalovic 90* (CONC); Bahía Santiago, *Cunningham in 1867* (S); Neighborhood of Monte Dinero, 52°19'S, 68°36'W, *Cunningham in 1868* (NY); 80 km NE of Punta Arenas, 25 m, *Eyerdam et al. 23935* (G, GH, NA, UC); Mina Loreto, near Punta Arenas, 150 m, *Mexia 7979* (BM, GB, GH, K, MO, NY, S, UC); Isla Riesco, Estancia Río de Los Palos, 53°26'S, 73°30'W, *Pfister & Ricardi in 1952* (CONC); Fiordo Silva Palma, Angostura Titus, Río Raul, *Pisano 3752* (HIP, MO, RNG); Seno Skyring, Estancia Skyring, *Pisano 4383* (HIP, MO); 8 km W of Aguas Frescas, 100 m, 53°20'S, 71°05'W, *Solomon 4685* (MO); Laguna Parrillar, 350 m, 53°20'S, 71°08'W, *Solomon 4686* (MO); 2 km W of Puerto Hambre, 20 m, 53°40'S, 70°55'W, *Solomon 4689* (MO). *Tierra del Fuego*, Bahía San Felipe, *Cunningham in 1867* (K); Estancia Vicuña, Cerro Bahamondes, 300 m, *Goodall 1756* (MICH, NA, RNG, UC, US); South of Cerro Sombrero, 52°46'S, 69°18'W, *Goodall 2060* (LTR, NA); Bahía Inútil, Estancia Camerón, 53°38'S, 69°39'W, *Moore 1076* (CAS, GH, RNG); Lago Blanco at Río Blanco, *Moore 1098* (CAS, RNG); Aserradero Río Bueno, 53°40'S, 69°55'W, *Pisano 2486* (CONC, HIP, RNG); Río Fontaine, 54°29'S, 68°59'W, *Skottsberg 122* (UPS). *Última Esperanza*, Estancia Cerro Castillo, Lago Porteño, *Moore 1023* (DS, RNG, S, SGO); Estancia Bories, Lago Escondido, 51°55'S, 72°09'W, *Moore 1028* (DS, RNG, US); Río Rubens, *Kalela 2088* (H); 2 km E of Puerto Cóndor, 51°38'S, 72°40'W, *Solomon 4703* (MO); Estancia Cerro Castillo, Lago Sofia, 51°32'S, 72°37'W, *T.B.P.A. (Latour et al.) 1508* (BAB, MO); Seno Última Esperanza, Puerto Toro, 51°25'S, 73°04'W, *T.B.P.A. (Moore & Pisano) 1896* (BAB, MO, RNG).

FALKLAND ISLANDS, Without locality, *Hooker in 1842* (BM, E, G, K, P). EAST FALKLAND: Goose Green, ca. 3 mi SE of Bodie Creek House, *Moore 612* (RNG); Darwin, *Moore 640* (DS, GH, LP, S, UC). Port Harriet, *Wright* (K). WEST FALKLAND: Fox Bay, *Vallentin in 1910* (K).

In southern South America, *Epilobium ciliatum* subsp. *ciliatum* is an extremely widespread, weedy, highly polymorphic taxon. Despite its variable nature, this species possesses many features that clearly distinguish it from other taxa. Most plants produce turions or leafy rosettes below or at the ground surface as overwintering structures, a feature that is not present in any other native South American species. This, combined with the presence of seeds with longitudinal lines of fused, flattened papillae, erect glandular-pubescent inflorescences, and small white to pink flowers, serves to separate *E. ciliatum* from other species with which it might be confused. Two species in particular, *E. obscurum* and *E. australe*, are often mistaken for *E. ciliatum*, especially when the specimens lack underground parts. *Epilobium obscurum* produces leafy basal shoots and has a densely strigillose inflorescence with glandular hairs restricted to the floral tube, rose purple petals, and narrowly lanceolate, denticulate leaves. Some plants of *E. ciliatum* from higher elevations or exposed sites are especially easy to confuse with *E. australe*, because their leaves are relatively small with few teeth, more congested, thicker, and the plants often are low in stature (less than 20 cm). *Epilobium australe* is shortly rhizomatous with leafy basal shoots; it completely lacks glandular pubescence and has thick, few-toothed, ovate leaves. *Epilobium obscurum* and *E. australe* have seeds without lines of fused papillae.

Many names have been given to the forms of *E. ciliatum* in South America. Most of these were proposed at a time when the number of collections was small, and each of the taxa appeared more or less homogeneous. For example, *E. chilense* was based on large-leaved, robust, densely glandular plants from central Chile, while *E. valdiviense* was drawn from specimens from the same area that were more graceful, less pubescent, with the leaves shorter than the internodes. In his monograph, Haussknecht (1884) recognized only three taxa in this complex

in South America. Subsequently, other names were proposed piecemeal for more or less distinctive populations or because of a lack of literature or understanding of previously published names.

Samuelsson (1923) recognized all of Haussknecht's taxa plus two others and, in addition, proposed five new species. These new taxa were either from remote areas or had distinctive morphological features that separated them from the other taxa with which Samuelsson was familiar. He placed a great deal of emphasis on the density of pubescence, leaf size and disposition, and branching patterns in separating his taxa; these features are extremely plastic within this subspecies.

The relationship of South American collections to North American taxa has been uncertain historically. Haussknecht, in his original description of *E. adenocaulon*, listed a collection from Aconcagua Prov., Chile (*R. Philippi*, W) among the four collections cited, with the other three from North America (Haussknecht, 1879). Later, in his monograph (Haussknecht, 1884), he re-identified this specimen as *E. chilense* but then cited a collection from Missoula, Montana (*Krause*, JE) under the latter name. Samuelsson (1923) later reassigned the Montana plants to *E. adenocaulon*. Apparently after publication of his monograph, Haussknecht annotated a few additional collections from Chile as *E. glandulosum* (Reiche, 1898) and *E. adenocaulon* (e.g., Castro, Chiloé Prov., Chile, *Gay* 63, P).

The relationship of the South American populations to those in North America was brought up again when it was learned that the seeds of *Epilobium chilense* shared a peculiar feature, the presence of longitudinal ridges of flattened, fused papillae, with the *E. ciliatum* complex (*E. ciliatum*, including *E. glandulosum* and *E. watsonii*; and *E. oreganum*; Seavey et al., 1977). This, combined with fleshy-leaved turions in both South and North American plants, strongly suggested that *E. chilense* was very closely related to *E. ciliatum*, if not conspecific (Seavey & Raven, 1977c).

Hoch (1978) examined the *Epilobium ciliatum* complex in North America, especially *E. ciliatum* itself. Plants of this species had long gone under a plethora of names, in particular *E. adenocaulon* and *E. glandulosum*. Hoch's study made it clear that the many taxa recognized from North America could not be recognized and still maintain a functional, information-rich taxonomy. As a result, *E. ciliatum* was reduced to a series of three modally and geographically distinct but intergrading subspecies.

In light of the careful work of Hoch and an examination and comparison of the bulk of the available South American material with a broad spectrum of North American populations, it is clear that the many taxa proposed from South America can be reduced to the single variable taxon *E. ciliatum* subsp. *ciliatum* as circumscribed by Hoch (1978). Indeed, some plants are almost indistinguishable (e.g., Yellowknife, Mackenzie Territory, Canada, *Cody & McCanse* 3327, MO, and near Paso Puyehue, Osorno Prov., Chile, *Solomon* 4593, MO; Kyle Canyon, Charleston Mtns., Clark Co., Nevada, *Goodman & Hitchcock* 1707, MO, and Vegas Blancas, west of Angol, Malleco Prov., Chile, *Solomon* 4450, MO; Rattlesnake valley, Missoula Co., Montana, *Barkley* 1887, MO, and Cerro Tronador, Río Negro Prov., Argentina, *Solomon* 4640, MO; Drummond Is., Chippewa Co., Michigan, *McVaugh* 9143, MO, and Río Blanco, north end of Lago Blanco, Tierra

del Fuego Prov., Chile, *Moore 1098*, RNG; Hawks Ranch, 25 mi S of Laramie, Albany Co., Wyoming, *Churchill in 1918*, MO, and between Cerro Blanco and La Hollada, Córdoba Prov., Argentina, *Solomon 4096*, MO; Ruby River, 30 mi S of Varney, Madison Co., Montana, *Parker 7033*, MO, and 8 km W of Aguas Frescas, Magallanes Prov., Chile, *Solomon 4685*, MO). These examples cover the full range of overlapping morphological characters found in North and South American plants, from simple to branched, densely glandular-pubescent to sparsely strigillose, and in size from 4 cm to over 40 cm.

Although there is considerable overlap in morphological features, two components, leaves and turions, are modally slightly different from populations in North America. The majority of South American plants produce fleshy-leaved turions just below the ground surface. This is especially prevalent at higher elevations and latitudes. Plants with leafy rosettes at the ground surface are found throughout the range. However, they form only a small portion of the plants from the southern part of the distribution of *Epilobium ciliatum* and are only frequent in the northernmost populations and in the coastal mountains and at low elevations (i.e., below about 1,000 m). Similarly, the leaves of plants from higher elevations and latitudes in South America show a tendency to be slightly thicker, generally shorter and proportionately broader, with fewer marginal teeth than many North American populations. Again, this is only a trend, with plants of very similar morphology appearing in North America, but not as often. The same trend from leafy rosettes toward condensed turions is also seen in North American populations, especially in cold or extreme habitats (Hoch, 1978).

In general, although *E. ciliatum* subsp. *ciliatum* in South America is quite variable, the overall diversity of morphological types represented is not as great as that found in North America and many of the conspicuously distinctive morphological types now included in subsp. *ciliatum* of North America are not present (e.g., *E. holosericeum*, *E. ecomosum*). It seems most likely that *E. ciliatum* is a fairly recent, possibly late Pleistocene or even Holocene, arrival in South America by means of long-distance dispersal. While it has diversified to some extent, the reduced variability of morphological types encountered probably reflects the relatively limited genotypic diversity of its founding population.

The most extreme range of variability in *E. ciliatum* is found in stature and branching patterns. Not only do these differ from one population to the next, but they are usually conspicuous within populations, depending on the location of an individual: in shade or full sun, at the edge of a stream, in a bog, or on a drying gravel bar. Plants are often simple, especially when small, but generally branch above or from below later in the growing season. Secondary branching can be extremely dense and prolific when the terminal shoot is damaged, giving the plants a bushy appearance. Low plants, ca. 15 cm tall, with this type of branching formed the basis of the name *E. magellanicum*.

Since *E. ciliatum* is perennial, turions or leafy rosettes as overwintering structures are produced late in the season. The dead scales of the previous year's turions usually persist around the base of the stem, often several centimeters under the ground surface, but these are frequently lost when specimens are gathered. Because *E. ciliatum*, like most other *Epilobium* species, will germinate, grow, and reproduce in a single season, many plants collected early in the growing

season or on newly formed, disturbed sites may appear to be annual, without any indication of perennating structures. It is certainly possible that individuals in particularly marginal habitats may be facultatively annual and do not produce overwintering structures at all.

Within a given population there is frequently an enormous disparity in size of the individuals. For example, an extensive population at the Termas de Chillán, Ñuble Prov., Chile (Solomon 4373, 4376) produced plants from less than 6 cm to more than 60 cm tall, all actively flowering and producing fully mature capsules. There were many more small and medium-sized individuals than large ones. This pattern is frequent throughout the range of *E. ciliatum* although not necessarily in every population.

Variation in the size of herbaceous plants has always posed a problem for taxonomists, especially when dealing with limited material that does not cover the full range of morphological diversity. Per Dusén described *Epilobium santa-cruzense* from several dozen plants between 5 and 10 cm tall, collected "in uliginosis" from the upper valley of the Río Santa Cruz. He compared them with *E. anagallidifolium*, but suggested that their seeds were very similar to *E. saximontanum*, a member of the *E. ciliatum* complex. Although these plants are quite distinctive when taken by themselves, they have been retained in *E. ciliatum* because populations from slightly further west around Lago Argentino (Solomon 4653, 4658, MO) contain plants of very similar morphology as well as a continuously intergrading series of larger plants. The seeds of *E. santa-cruzense* have the conspicuous ridges typical of *E. ciliatum*.

The extent to which size differences, as seen in *Epilobium ciliatum*, are genetically controlled is not known. In a recent study of an annual, out-crossing species of *Stephanomeria*, Gottlieb (1977) showed that there was no apparent genetic difference between small and large members of a single population, and that size and seed production were regulated by environmental factors.

It is certainly possible that a similar situation occurs in *Epilobium ciliatum*. In a series of collections from Villa Cerro Catedral, Río Negro Prov., Argentina (Solomon 4613, 4614, 4615, MO), plants from a level sandy area, which had once been wet, were mostly less than 7 cm tall, with small flowers and densely leafy stems. Only a few meters away, at the edge of a small stream, plants 30 to 40 cm tall, with long internodes and larger flowers were found. In between were plants of intermediate stature, their size apparently depending on the available soil moisture. The high rate of autogamy in *E. ciliatum* undoubtedly must have some impact on the genotypes available for each succeeding generation, but its significance is not known. A study similar to that conducted on *Stephanomeria exigua* Nutt. would be well worth the investigation.

Stem vestiture also shows significant variation. In general, *Epilobium ciliatum* has both glandular and strigillose pubescence, although both types may be sparse, or the glandular hairs may be restricted to just the ovaries. Only rarely are completely glabrous plants encountered, such as those on which Samuelsson based his *E. leiophyton*. The density of the glandular pubescence seems to have some geographical basis. Plants from lower elevations in the central valley and coastal range in the northern portion of the Chilean distribution (mostly north of Valdivia) are often densely glandular-pubescent (e.g., Concón, Valparaíso Prov., Chile,

Garaventa 500; Limache, Quillota Prov., Chile, *Looser 2007, 2011*; Corral, Valdivia Prov., Chile, *Gunckel 15169*; 44 km E of El Colorado, Talca Prov., Chile, *Solomon 4339*; 30 km W of Curacautín, Malleco Prov., Chile, *Solomon 4473*). Within this distribution, densely glandular plants are frequent and often characterize entire populations. At higher elevations and further to the south, glandular hairs are less dense, and the dense type does not appear in Argentina at the same latitude. Although pubescence is not an insignificant feature and does apparently have a geographical basis, it is not useful to recognize these plants in a formal way, because the variation in other characters is indistinguishable from that found in other populations, and pubescence density is often a quantitative and plastic character. The only evident correlation for the presence of densely glandular plants may be due to their occurrence in the warmest and driest portions of the range of *E. ciliatum* in South America, although the functional significance of most hair types in plants is very poorly known (Ehleringer et al., 1976; Levin, 1973).

Epilobium ciliatum typically has small, highly autogamous flowers that show little variation in size. Like the turions and leaves discussed earlier, the color of the petals also varies geographically. Low-elevation plants from the central valley and coast range of central Chile have white flowers that flush only a faint pink, or not at all, after anthesis. Those from higher places in the Andes at this same latitude are also usually white at anthesis, but these may fade to a darker pink afterward. As one moves southward along the Andes, beginning in the vicinity of San Carlos de Bariloche, plants with pink flowers at anthesis become increasingly common, so that populations from Santa Cruz Prov., Argentina, adjacent Chile, and Tierra del Fuego are all pink flowered. Pink flowered populations may also be found further north, but only at higher elevations. The pink petal color is produced by malvidin-3-5-diglucoside (Harborne, 1967), the presence and abundance of which, in the case of *E. ciliatum*, is possibly environmentally controlled. The genes that control pigment production are perhaps induced under the influence of decreasing temperatures, or increased ultraviolet radiation at high elevations or latitudes. Transplants of turions from pink flowered plants (Ushuaia, Tierra del Fuego, Argentina, *Solomon 4712*; grown as M1856 in 1979), under greenhouse conditions, produced white flowers. Seed from two other pink flowered populations (near Ventisquero Perito Moreno, Prov. Santa Cruz, Argentina, *Solomon 4656, 4658*; grown as M1850, M1851, in 1979, respectively) also produced only white flowers under greenhouse cultivation.

It is not surprising that a weedy, autogamous species such as *Epilobium ciliatum* should exhibit a substantial amount of variation, both between populations and within a single population. The often disturbed habitats where *E. ciliatum* occurs, such as stream beds, seep, or embankments, over a broad elevational range, are ephemeral, being newly created or altered from one year to the next, and often in a drastic manner, by such agents as flooding. The ability to successfully colonize these localities requires not only high dispersability, but also great genotypic and phenotypic plasticity to cope with a broad spectrum of environmental parameters. It may be safely said that *E. ciliatum* is a superlative example of such an opportunistic species.

Disjunct populations of *Epilobium ciliatum* are found in the Sierra de San Luis

and the Sierra Grande de Córdoba. These undoubtedly originated by long-distance dispersal of seed from the main range of the Andes via the westerly winds. Some of the most robust and largest leaved individuals seen in any population came from the Sierra Grande, where they were found growing in moist ravines (Solomon 4074, 4096). All of the populations examined in the Sierra Grande had white flowers. Disjunct populations also occur in the Falkland Islands and must have been derived in a similar fashion from populations to the west. Apparently, *E. ciliatum* is rare and scattered along streams on these islands (Moore, 1968).

Epilobium ciliatum is by far the most common species encountered in the central and southern Andes of Chile and Argentina, where it grows sympatrically with at least nine other species. It overlaps with *E. hirtigerum* and *E. denticulatum*, in the Sierra Grande, and with the latter also in a narrow band along the east side of the Andes in Mendoza and San Juan provinces, Argentina, and in the Sierra de San Luis.

Despite the highly autogamous or even functionally cleistogamous flowers, occasional hybrids with *Epilobium australe*, *E. barbeyanum*, *E. denticulatum*, *E. glaucum*, *E. hirtigerum*, *E. obscurum*, and possibly *E. puberulum* do occur. Only hybrids with *E. australe* and *E. glaucum* are discussed here, because they are the most frequently encountered, in part due to their broadly sympatric range with *E. ciliatum* throughout the southern Andes. Details on the other hybrids are found under each of the other species listed above.

All of the species that hybridize with *Epilobium ciliatum*, except *E. denticulatum* and *E. puberulum*, have the BB chromosome arrangement. Hybrids between the two chromosomal groups are usually easily distinguished because of the intermediate morphology and reduced seed set and pollen stainability. Hybrids between *E. ciliatum* and *E. glaucum* (e.g., Arroyo Huelta, Lago Nahuel Huapi, Solomon 4626, 4627, MO; and Cerro López, Río Negro Prov., Argentina, without collector in 1953, BAB) generally have narrow, few-toothed leaves, strigillose pubescence, sometimes with glandular hairs, and loose, elongate turions. The average pollen stainability for Solomon 4626, 4627, and the Cerro López collection was 21%, 19%, and 22%, respectively.

Hybrids between *Epilobium ciliatum* and *E. australe* are more difficult to distinguish, but the reduced seed set or poor capsule development is an indicator of hybrid origin. In hybrids of this combination (e.g., Ea. Achalay, Santa Cruz Prov., Argentina, T.B.P.A. 2349, MO, RNG; Río Coyle, Santa Cruz Prov., Argentina, Dauber 4, BAA; and Arroyo Beta, Tierra del Fuego, Argentina, Castellanos in 1942) have intermediate leaf morphology, usually a few glandular hairs, larger pink flowers, good seeds with few, imperfectly formed ridges, and loose, somewhat elongate leafy basal shoots. The average pollen stainability for Dauber 4 (BAA), T.B.P.A. 2349 (MO, RNG), and Castellanos in 1942 was 19%, 22%, 28%, and 30%, respectively.

6. ***Epilobium nivale*** Meyen, Reise um die Erde 1:315. 1834. Walp., Reliq. Meyen, 327. 1843. TYPE: Chile, VII Región (Maule), Cerro Imposible, 3,800 m, January–March 1831, F. Meyen (JE, lectotype here designated, photograph MO; B (destroyed, photographs BH, GH, MO, NY), BR, K, P, W, isoelectotypes). Gay, Hist. Fis. Chile 2:349. 1846. Walp., Repert. Bot. Syst. 5:666. 1846. Hausskn.,

Monogr. *Epilobium* 251. 1884. Reiche, Fl. Chile 2:244. 1898. H. Lév., Iconogr. *Epilobium*, tab. 205. 1911. Samuelsson, Svensk Bot. Tidskr. 17:290. 1923.

E. alpinum auct. non L.: Hook. & Arn., Hook. Bot. Misc. 3:390. 1833.

E. andinum R. Phil., Anal. Univ. Chile 84:747. 1893. TYPE: Chile, VII Región (Maule), Cordillera de Talca, Cuesta de Las Animas, February 1879, F. Philippi (SGO-53014, lectotype here designated, photographs GH, MO; SGO-41463, SGO-53021 (specimen in upper right portion of sheet), probable isoelectotypes). Philippi's handwritten annotation of *Epilobium andinum* has been seen on six herbarium sheets at SGO, representing three different species, *E. nivale*, *E. australe*, and *E. ciliatum* subsp. *ciliatum*, all potential types for the name *E. andinum*. That all three species were included in the protologue is evidenced by:

1. "El ejemplar más grande del herbario mide 19 centímetros, . . ." (The largest specimen in the herbarium measures 19 cm, . . .). There is one specimen, SGO-53019, which is about 19 cm tall, a collection of *E. ciliatum* subsp. *ciliatum*.

2. "Los ejemplares de la Cordillera de Talca y de La Cueva (Sierra Velluda) son menos altos y echan muchas ramas en su base" (The specimens from the Cordillera de Talca and La Cueva (Sierra Velluda) are smaller and produce many branches from the base). The specimen from La Cueva, SGO-53020, is an example of *E. australe*.

3. In the Latin diagnosis, R. Philippi begins with, "Epilobium glaberrimum; caule tereti; foliis omnibus oppositis, . . ." There are three specimens of *E. nivale*, SGO-53014, SGO-41463, and SGO-53021 in upper right, all of which are glabrous and have consistently opposite leaves. Among native South American *Epilobium*, only *E. nivale* and the distinctive *E. glaucum* are glabrous. Based on the Latin diagnosis, it appears that Philippi had the specimens of *E. nivale* specifically in mind, even though he included specimens of two other species in his discussion.

Low, caespitose perennial herb, (5–)10–20(–30) cm tall, from a fibrous root system. Stems numerous, decumbent, terete, simple, occasionally branched above, usually reddish purple throughout or bicolored reddish purple on the upper surface and green on the lower, glabrous. Leaves mostly opposite, alternate only in the inflorescence, thick, dark green, often reddish purple along the margins, narrowly ovate to lanceolate, 0.5–1.6(–2.5) cm long, 1.5–5(–8) mm wide, acute or occasionally obtuse at the apex, remotely denticulate with 1–4 low teeth on each side, acute to cuneate at the base, glabrous, the lateral veins very inconspicuous, none or 1, rarely 2, on each side of the midrib, on petioles 0.5–1 mm long. Inflorescence erect, simple. Flowers erect. Ovaries reddish purple or occasionally bicolored, reddish purple on one half, green on the other, glabrous, 0.5–1.2 cm long, on pedicels 1–6 mm long. Floral tube often reddish-purple, 0.5–0.8 mm deep, 1.2–2 mm wide, glabrous. Sepals often reddish purple, lanceolate, 1.9–2.8 mm long, 0.8–1.3 mm wide, glabrous. Petals pale pink, 2.8–4.5 mm long, (1–)1.4–2.2 mm wide, the notch 0.5–0.9(–1.2) mm deep. Anthers cream, 0.4–0.6 mm long, 0.4–0.5 mm wide; filaments cream, those of the longer stamens 1–1.6 mm long, those of the shorter 0.4–0.8 mm long, the longer stamens shedding directly on the stigma at anthesis. Style cream to white, 1.2–1.6 mm long; stigma cream to white, subcapitate to clavate, 0.6–1.5 mm long, 0.5–0.8 mm thick. Capsules erect, often reddish purple, occasionally bicolored, reddish purple on one half, greenish or light brown on the other, glabrous, 1.1–4 cm long, on pedicels 0.3–1.2(–1.8) cm long. Seeds pale brown, papillose, obovoid, 1.1–1.4 mm long, 0.3–0.5 mm thick, the chalazal end with an appendage, 0.04–0.1 mm long, 0.08–0.15 mm wide; coma white, 2.5–7 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 5): Along rivulets, boggy places, stream banks, and other permanently wet sites in alpine areas, often extending upward to the snow line, occasionally on stable scree, and sometimes extending to slightly lower elevations, especially in the forest regions, along rocky stream beds. In the central

and southern Andes of Chile and Argentina from Paso Portillo (33°S), southward along the mountains to the vicinity of Epuyén, Chubut Prov., Argentina, disjunct to the Torres del Paine region of Chile and Lago Argentino, at elevations of 2,000–3,500 m in the northern portion of its range, gradually descending to 1,200–2,000 m in Río Negro and Chubut, and in the southernmost populations from 350 to 1,200 m. Flowering December to March.

Representative specimens examined: ARGENTINA, CHUBUT: Epuyén, Cuartel Epuyén, *Lourteig & Buchinger* 22 (P). MENDOZA: Valle Atuel, Lago Atuel, 3,100 m, *Böcher et al.* 1972 (C, DS); Dpto. Las Heras, Las Cuevas, 3,220 m, *Boelcke* 9766 (BAA, BAB, MO); Dpto. Malargüe, Paso Pehuenche, *Boelcke et al.* 10358 (BAA, BAB, MO); Arroyo en el alto valle, Calmucó, 36°24'S, 69°50'W, *Burkart et al.* 14178 (LIL); Tres Esquinas, 33°50'S, 69°00'W, *Carette* 285 (LP, SI); Laguna Diamante, 3,200 m, *Carette* 286 (LP, SI), *Serra* 39 (LP); Valle del Atuel, Cajón del Burro, *Gerth* 108 (L, SI); Valle Hermoso, *Kurtz* 5860 (CORD, G, JE, NY), *Sosa* 13 (SI); Dpto. Malargüe, entre Arroyo Alverjalito y Arroyo Leñas Amarillas, *Kurtz* 7160 (CORD, JE, SI); Dpto. San Rafael, Arroyo El Indigeno, 10 km N of Volcán Overo, *Lagiglia* 2218 (LP); Dpto. Tunuyán, Valle del Alto Tunuyán, Paso Hondo, *Leal* 2059 (LIL); Dpto. San Rafael, Cerro de Los Molles, *Kurtz* 7514 (CORD, JE, LP), *Rossi* 297 (LIL); *Sleumer* 637 (B, LIL). NEUQUÉN: Parque Nacional Nahuel Huapi, Cerro Colorado, entre Pto. Manzano y Lago Traful, *Boelcke & Correa* 6909 (BAA, BAB); Norquinco, 2,200 m, 39°08'S, 71°18'W, *Comber* 539 (K); Dpto. Lácar, Cerro Chapelco, 1,800 m, *Cabrera* 23009 (LP), *Correa et al.* 5886 (BAB, MO); Copahue, 1,000 m, *Kraftsik in* 1968 (BAB). Paso Pino Hachado, *Parodi* 2215 (BAA); Lago Villarino, 40°26'S, 71°36'W, *Roth in* 1896 (LP). RÍO NEGRO: Cerro Tronador, Río Manso Superior, *Gentili in* 1975 (MO); Cerro Utne, 41°19'S, 71°21'W, *Hosseus* 456 (CORD), 463 (CORD); Parque Nacional Nahuel Huapi, Cerro Catedral, 2,000 m, *Pedersen* 1488 (C); Cerro V. López, W of Bariloche, 1,500 m, 41°05'S, 71°35'W, *Solomon* 4620 (MO). SANTA CRUZ: Estancia Lago Roca, Cerro Fraile, 50°32'S, 72°39'W, *James* 427 (BM, DS); Lago Argentino, Cerro Buenos Aires, 50°24'S, 72°59'W, *James* 711 (BM), *Skottsberg* 945 (UPS); Dpto. Güer Aike, Estancia Las Viscachas, 1,250 m, 50°46'S, 72°08'W, *T.B.P.A. (Arroyo et al.)* 2671 (RNG).

CHILE, V REGIÓN (ACONCAGUA): *Los Andes*, Juncal, 32°52'S, 70°10'W, *Buchtien in* 1903 (US); Laguna del Inca, *Kurtz in* 1886 (JE, LP, NY); Paso Portillo, 2,800 m, *Milner in* 1935 (CONC), *Sparre* 1687 (S), *Wall in* 1946 (A, S). REGIÓN METROPOLITANA (SANTIAGO): *Cordillera*, Vegas del Tupungato, *Behn in* 1930 (CONC), *Melin in* 1930 (UC); Cerro de San Pedro Nolasco, 33°48'S, 70°16'W, *Gillies* (BM, E, OXF); Laguna Negra, *Vidal in* 1873 (SGO); Ski village La Parva, 2,850 m, 33°20'S, 70°18'W, *Moore* 395 (LA, MO), *Solomon* 4361 (MO). VI REGIÓN (O'HIGGINS): *Cachapoal*, Sewell, 2,400 m, *Bastin* 16 (US); Cauquenes, *Gay* 188 (P); Río Coya above El Teniente, 2,700 m, *Pennell* 12292 (F, GH, NY, PH, SGO); Ventisquero Los Cipreses, 2,000 m, *Reed in* 1872 (POM). *Colchagua*, Cordillera de Colchagua, 2,000 m, *Pirion* 107 (GH). VII REGIÓN (MAULE): *Curicó*, Cajón del Azufre, *Albert in* 1891 (SGO); 20 km oeste del Paso Vergara, *Calderón in* 1967 (CONC); Laguna de Teno, 2,500 m, *Martcorena & Matthei* 841 (CONC). *Linares*, Cordillera de Linares, *Philippi in* 1862 (G, HAL, S); Termas de Longaví, *Schumann in* 1888 (SGO). *Talca*, Laguna del Maule, *Aravena* 1021 (UC), *Ricardi et al.* 969 (CONC, MO). VIII REGIÓN (BÍO-BÍO): *Bío-Bío*, Cordillera de Antuco, La Cueva, *Rahmer in* 1887 (SGO). *Nuble*, Termas de Chillán, *Jaffuel* 3728 (GH), *Pennell* 12413 (F, GH, NY, PH), *Solomon* 4372 (MO). IX REGIÓN (ARAUCANÍA): *Malleco*, Termas del Río Blanco, 1,300 m, 38°35'S, 71°35'W, *Solomon* 4504 (MO). XII REGIÓN (MAGALLANES): *Última Esperanza*, Estancia Cerro Paine, 50°59'S, 72°58'W, *Pisano* 4344 (HIP, MO).

Epilobium nivale is a distinctive, high montane species, readily recognized by its glabrous, delicate, decumbent, clumped or somewhat caespitose stems, with few, small pink flowers. Only *E. glaucum* and some individuals of the introduced *E. paniculatum* are also glabrous, but they are much more robust and erect. The small pink flowers are often functionally cleistogamous, because they open partially or not at all on cloudy days, and only for a few morning hours on sunny days.

Epilobium nivale grows sympatrically with four other species, but only rarely is there evidence to suggest interspecific hybridization. Hybrids with *E. australe* and *E. densifolium* would be difficult to distinguish from small-leaved forms of those species, except perhaps in flower size. Recognizable hybrids involving *E.*

ciliatum have not been found, and only a single collection from Termas de Chillán, Prov. Ñuble, Chile (Solomon 4372, MO) exhibits a tendency toward larger, acuminate leaves and the more erect stems characteristic of *E. glaucum*. This specimen, however, had a pollen stainability of 96%, which is substantially different than the stainability of artificial hybrids between these species.

Ecologically, *E. nivale* occurs in the same habitats and community associations in the southernmost disjunct populations as it does in, for example, the vicinity of Lago Nahuel Huapi; that is, in wet places at the upper limits of *Nothofagus pumilio* (Poepp. & Endl.) Krasser scrub and at higher elevations. In the Torres del Paine region, at elevations approaching 1,000 m, *E. nivale* is apparently the only species found in permanently wet places (Pisano, 1974, as *E. conjungens*). Farther north, beyond the limits of the *Nothofagus* forest, *E. nivale* continues to appear in permanently wet sites, but at increasing elevations.

7. ***Epilobium barbeyanum*** H. Lév., Bull. Herb. Boissier, sér. 2, 7:589. 1907. TYPE: Chile, IV Región (Coquimbo), Vegas del Toro, Cordillera de Coquimbo, 2,500 m, 1 February 1883, F. Philippi (?) (G, holotype, photograph MO; JE, SGO-53122, isotypes). The specimen at G is accompanied by a letter from F. Philippi dated 29 May 1883, and the specimens were probably collected by him. H. Lév., Repert. Spec. Nov. 9:19. 1910–11. Samuelsson, Svensk Bot. Tidskr. 17:265. 1923; Svensk Bot. Tidskr. 24:4. 1930.

Perennial herbs (8–)15–40 cm tall, overwintering and reproducing vegetatively by elongate leafy shoots or soboles produced from the base. Stems erect ascendent or decumbent, terete, usually simple or sparingly branched throughout, abundantly branched from the base, densely pubescent throughout with erect glandular hairs, 0.1–0.2 mm long, with an admixture of strigillose hairs, 0.1–0.2 mm long, in descending lines from the petiole bases or scattered in the inflorescence. Leaves mostly opposite, usually alternate in the inflorescence, the internodes often elongate and the leaves remote in fruit, thin, bright green, lanceolate to narrowly ovate, (0.6–)1–2 cm long, 0.2–1 cm wide, acute to acuminate, rarely obtuse at the apex, remotely denticulate with 3–5 teeth on each side, the margin frequently undulate, acute to obtuse or occasionally rounded at the base, with erect glandular hairs on both surfaces, usually with an admixture of strigillose hairs on the adaxial midrib and margins or thinly scattered on both surfaces, glabrate with age, the lateral veins obscure, 2–4 on each side of the midrib, on poorly defined petioles 0–1 mm long. Inflorescence erect, simple, the leaves subtending the flowers undifferentiated or slightly reduced in size. Flowers erect. Ovaries densely covered with erect glandular hairs, with an admixture of strigillose hairs, these also often dense, 0.9–1.5 cm long on pedicels 1–5 mm long. Floral tube 0.8–1.5 mm deep, 1.3–2(–2.7) mm across, externally with erect glandular and scattered strigillose hairs, internally with a conspicuous ring of erect villous hairs, 0.15–0.2 mm long near the base. Sepals lanceolate, 2.5–3.2(–4) mm long, 0.9–1.5 mm wide, with erect glandular and scattered strigillose hairs. Petals pale pink, obovate, 4–6 mm long, 2.5–3.4 mm wide, the notch 1–1.7 mm deep. Anthers cream to white, 0.6–1 mm long, 0.5–0.7 mm wide; filaments cream to white, those of the longer stamens 1.5–2(–3) mm long, those of the shorter 0.6–

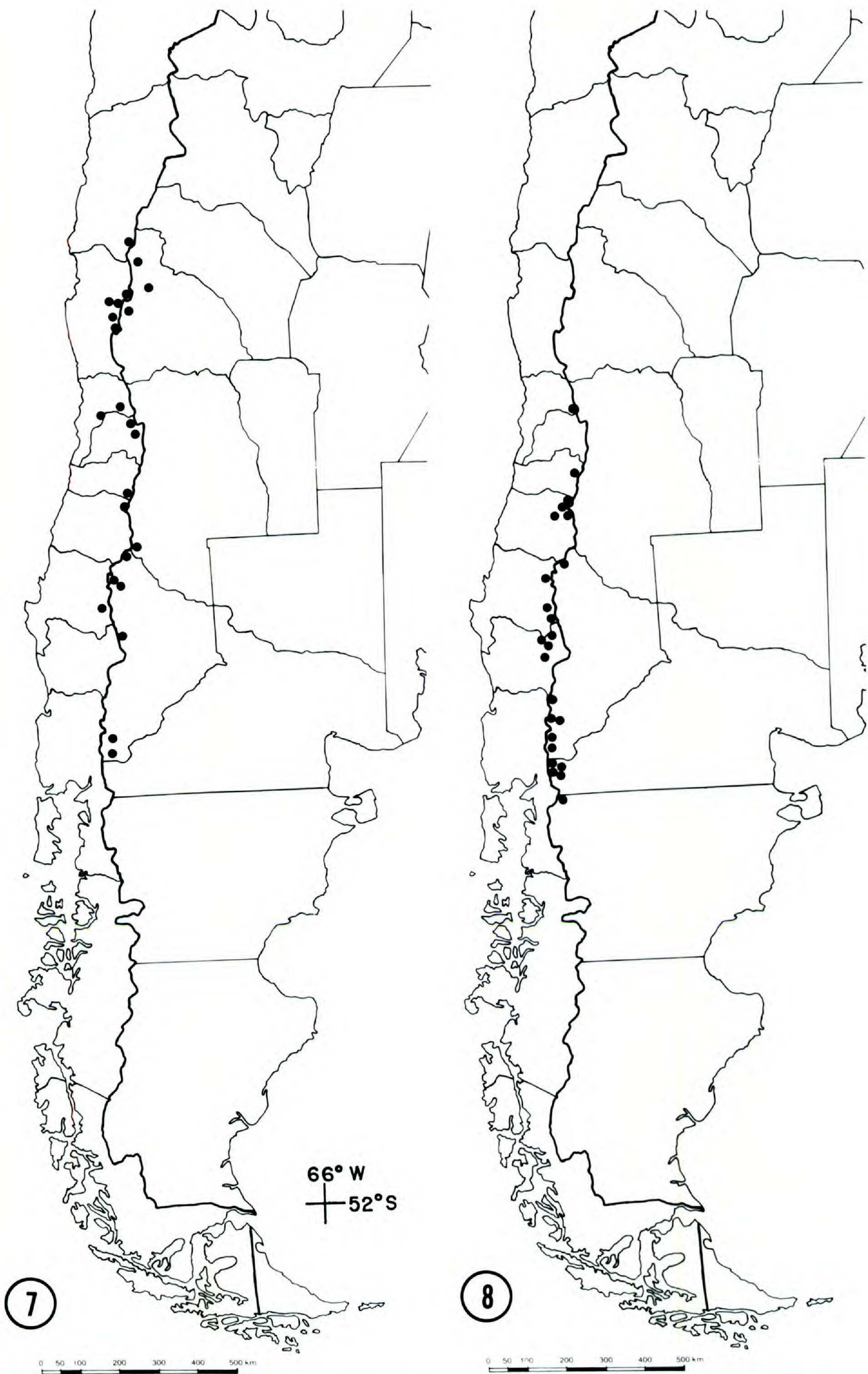
1(–1.9) mm long; the longer stamens shedding directly on the stigma at or shortly after anthesis, occasionally the shorter ones also. Style cream to white, capitate, 0.6–1 mm long, 0.6–1 mm thick. Capsules strictly erect, sparsely covered with erect glandular and scattered strigillose hairs, 3.4–5.2 cm long, 1.3–1.6 mm thick, on pedicels (0.5–)1.2–2.9 cm long. Seeds brown, papillose, obovoid, 0.85–1.3 mm long, 0.4–0.5 mm thick; coma white to slightly yellowish brown, 5–8 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 7): In very wet places in bogs, and along streams, sometimes partially submerged or floating; throughout the central Andes of Chile and Argentina, from southern III Región (Atacama), Chile, and central San Juan Prov., Argentina, southward to the vicinity of Lago Nahuel Huapi; also in the coast range (Cuesta La Dormida) between Santiago and Valparaíso, at elevations of 2,000–3,500 m in the north, gradually descending to 900–1,700 m in the southern part of its range. Flowering November to March.

Specimens examined: ARGENTINA, MENDOZA: Dpto. Malargüe, camino a Paso Pehuenches, Km 50, 1,800 m, *Cabrera et al.* 22831 (LP). NEUQUÉN: Dpto. Los Lagos, Estancia Fortín Chacabuco, *Boelcke* 4547 (BAA); Dpto. Minas, Arroyo Las Bandurria, entre Las Ovejas y Laguna Epulauquén, 1,250 m, 36°55'S, 70°56'W, *Boelcke et al.* 10788 (BAA, BAB, MO), *Ragonese* 225 (BA, RSA); Dpto. Minas, Laguna Epulauquén, 1,300 m, 36°50'S, 71°05'W, *Boelcke* 10906 (BAA, BAB, MO); Dpto. Chos Malal, Vegas del Pelán, 1,700 m, 36°54'S, 70°20'W, *Boelcke et al.* 11134 (BAA, BAB, MO); Dpto. Minas, Laguna Varvarco Campos, Arroyo Benítez, 36°17'S, 70°39'W, *Boelcke* 14224 (BAA, BAB); Traful, Estancia La Primavera, *Castellanos in 1938* (BA, RSA), *Gervóia in 1938* (LIL); Rahue, camino a Aluminé, *Dawson & Schwabe* 2180 (BAA, BAB, CTES); Paso Pino Hachado, *Hauman in 1920* (BA); Dpto. Loncopué, Cajón Chenque-Pehuén, 38°06'S, 70°55'W, *Rugolo & Agrasar* 172 (BAA, MO). SAN JUAN: Dpto. Calingasta, Manantiales, 3,500 m, *Fabris & Zuloaga* 8449 (LP), *Zardini* 180 (LP); Dpto. Iglesia, Río Blanco, Sierra San Guillermo, 3,200 m, 29°08'S, 69°30'W, *Hosseus* 1443 (CORD); Dpto. Calingasta, Cienaga de Las Cabeceras, 2,700 m, 31°47'S, 69°07'W, *Kurtz* 9806 (BAF, CORD), 9815a (CORD), *Spegazzini in 1937* (BAB); Dpto. Iglesia, Tudcum, *Perrone in 1950* (BA, MO).

CHILE, III REGIÓN (ATACAMA): *Huasco*, Quebrada Alfalfa, 2,800 m, 28°52'S, 69°49'W, *Johnston* 5996 (GH, S); Río de la Laguna Grande, 2,750 m, 28°44'S, 69°57'W, *Johnston* 6009 (GH, S). IV REGIÓN (COQUIMBO): *Choapa*, Río Illapel, without collector or date (K), *Volkman in 1860–61* (SGO); Quebrada La Vega Escondida, E of Cuncumén, 2,630 m, *Morrison & Wagenknecht* 17433 (GH, NA, UC), *Worth & Morrison* 16556 (NA, UC). *Elqui*, Laguna de Elqui, *Barros* 6616 (US); 6 km al oeste del Embalse La Laguna, 3,100 m, 30°13'S, 70°04'W, *Ricardi et al.* 1792 (CONC). *Limarí*, La Hualtata, 2,500 m, 30°39'S, 70°39'W, *Jiles* 1182 (CONC); Río Molles, 2,600 m, 30°44'S, 70°36'W, *Jiles* 1966 (CONC), *Jiles* 2098 (CONC); Río Flamencos, 2,700 m, 30°40'S, 70°23'W, *Jiles* 2914 (CONC); Potrero Grande, 2,700 m, 31°18'S, 70°50'W, *Jiles* 4837 (CONC). V REGIÓN (ACONCAGUA): *Los Andes*, Hacienda San Vicente, 2,000 m, 32°54'S, 70°37'W, *Martínez in 1968–69* (SGO). REGIÓN METROPOLITANA (SANTIAGO): *Cordillera*, Cordillera de Santiago, *Philippi* (G, mixed with *E. ciliatum*); El Refugio, on road to Lagunillas, 2,100 m, 33°40'S, 70°20'W, *Solomon* 4295 (MO), 4296 (MO). *Melipilla*, 3 km S of Las Vizcachas, La Dormida, *Morrison & Wagenknecht* 17110 (GH, UC). *Santiago*, Entre Maitenes y Pérez Caldera, 2,000 m, 33°11'S, 70°29'W, *Skottsberg & Sparre* 11063 (CONC, H, S); Road to Farellones, 2,050 m, 33°20'S, 70°18'W, *Solomon* 4285 (MO), 4360 (MO); Farellones, 2,200 m, *Wall & Sparre in 1947* (S). VI REGIÓN (O'HIGGINS): *Colchagua*, 25 km above La Rufina, road to Termas Vegas del Flaco, 1,450 m, 34°55'S, 70°30'W, *Solomon* 4320 (MO). VII REGIÓN (MAULE): *Curicó*, Cordillera del Planchón, *Née in 1793* (MA). VIII REGIÓN (BÍO-BÍO): *Bío-Bío*, Andes de Antuco, *Poeppig in 1828* (M, OXF; mixed with *E. australe*); Road to Laguna La Laja, 930 m, 37°25'S, 71°25'W, *Solomon* 4444 (MO). *Ñuble*, Cuchacucha, *Philippi* (JE).

Epilobium barbeyanum is most distinctive due to its dense, erect glandular pubescence throughout, the sparsely toothed, often undulate leaf margins, and the usually elongate leafy basal shoots. Only some populations of *E. ciliatum* and *E. denticulatum* are as densely glandular, but they have distinctive features, such as turions or spreading pubescence. Superficially, *E. barbeyanum* may resemble *E. australe* in leaf shape and habit but generally the leaves are more lanceolate,



FIGURES 7-8. Distribution of *Epilobium* species.—7. *E. barbeyanum*.—8. *E. densifolium*.

and *E. australe* completely lacks glandular pubescence. The elongate basal shoots (up to 25 cm long) are a result of growth in water-saturated or mucky soils in boggy places. In slightly drier situations at the edges of wet places, the plants may be much smaller and produce few or no basal shoots. The shoots and main stems are frequently densely intertwined, and often found floating or partly submerged, with the erect flowering portions elevated above the soil or water surface.

Hector L  veill   first described *Epilobium barbeyanum* while reviewing the epilobiums in Herbiers Boissier and Barbey-Boissier (L  veill  , 1907). His original description was very short and generalized enough that it would have been suitable for several species. Four years later, he published an amplified diagnosis of the single collection with which he was acquainted, citing for the first time the type locality (L  veill  , 1911).

Epilobium barbeyanum grows sympatrically with several species and occasionally forms hybrids. Plants clearly of hybrid origin between *E. barbeyanum* and *E. glaucum* have been collected from La Hierba Loca (Prov. Limar  , Chile, Jiles 4214, CONC; pollen stainability 35%). Two probable hybrids with *E. ciliatum* have also been seen, one from Las Cabeceras, Dpto. Calingasta, Prov. San Juan, Argentina, Spegazzini in 1937 (BAB), the other from Cerro Vizcachas, in the coast range between Santiago and Valpara  so, Chile, Schlegel 4987 (CONC; pollen stainability 47%). These hybrids are characterized by reduced seed set and pollen fertility, and an intermediate morphology most strongly reflected in the growth habit, leaf shape, and venation.

8. ***Epilobium densifolium*** Hausskn., Monogr. *Epilobium* 256, tab. 18, f. 77a–b. 1884. TYPE: “Chile bor. Andes, ad nives perpetuas,” without more precise locality, 1828, *E. Poeppig* (LE, holotype, not seen; JE, PR, UPS, isotypes). Probably from the Andes near Volc  n Antuco, where Poeppig collected extensively from November 1828 to early February 1829, although it cannot be definitely ruled out that the specimens could have been taken from the Andes above San Felipe, Los Andes Prov., during the first week of January 1828 on Poeppig’s return from Mendoza (Urban, 1896). Reiche, Fl. Chile 2:244. 1898.

E. pauciflorum R. Phil., Anal. Univ. Chile 84:748. 1893, non Schrank, Denkschr. K  nigl.-Baier. Bot. Ges. Regensburg 1(2):15. 1818, nec Dulac, Fl. Haute-Pyr. 332. 1867. TYPE: Chile, VIII Regi  n (B  o-B  o), Prov. B  o-B  o, Cordillera de Antuco, La Cueva, January 1887, C. Rahmer (SGO-41441, lectotype here designated, photograph MO; JE, isolectotype). Samuelsson, Svensk Bot. Tidskr. 17: 260. 1923; Svensk Bot. Tidskr. 24:11. 1930.

E. lignosum F. Phil., Anal. Univ. Chile 84:746. 1893. *E. nivale* var. *lignosum* (F. Phil.) Hosseus, Trab. Inst. Bot. Farm., Buenos Aires 33:56. 1915. TYPE: Chile, VII Regi  n (Maule), Prov. Curic  , Cuesta de Las Animas, 35  29’S, 70  52’W, 15 February 1879, F. Philippi (SGO-41440, lectotype here designated, photograph MO, drawing JE; SGO-53101, probable isolectotype, photograph MO). H. L  v., Iconogr. *Epilobium*, tab. 196. 1911.

Caespitose, clumped perennial herb, 10–25(–35) cm tall, usually with a long, contorted, more or less woody rootstock. Stems ascendent, numerous, simple, or occasionally few branched above, terete, strigillose throughout, with hairs 0.1–0.2 mm long, or glabrate below, then the pubescence mostly limited to descending lines from the petiole bases, densely leafy, often with fascicles of small leaves in the axils of stem leaves. Leaves mostly opposite, alternate only in the inflorescence, thick, green, occasionally glaucous, narrowly lanceolate to lanceolate,

0.5–2.4 cm long, 1.5–6 mm wide, acuminate or acute at the apex, subentire or remotely denticulate, with 1–3(–5) teeth on each side, acute to cuneate at the base, strigillose on both surfaces, or glabrate with age and then strigillose on the margins and the adaxial midrib, the lateral veins obscure, 2–3 on each side of the midrib, on poorly defined petioles 0–1.5 mm long. Inflorescence erect, simple, few-flowered, the leaves subtending the flowers only slightly, if at all, reduced in size. Flowers erect. Ovaries occasionally reddish, strigillose, 0.8–2 cm long, on pedicels (0.3–)0.5–1(–1.5) cm long. Floral tube 1.4–2.2 mm deep, 2–3 mm across, externally strigillose, internally with a ring of erect villous hairs 0.1–0.15 mm long near the base, rarely glabrous. Sepals lanceolate (4.2–)5–7.3 mm long, 1.2–2 mm wide, slightly keeled at the base, strigillose. Petals pale pink to rose purple, often the base of the petal paler than the apex, obovate, rarely broadly so, 7–12 mm long, 4–6(–7.5) mm wide, the notch (1.2–)2.3–3.2 mm deep. Anthers cream, 1–1.7 mm long, 0.5–0.8 mm wide; filaments cream, those of the longer stamens 2.2–3.5 mm long, those of the shorter 1.3–2.4 mm long; the anthers usually held away from the stigma at anthesis, usually the longer stamens bending and barely shedding on the lower part of the stigma after anthesis. Style cream, (2.2–)3.8–5.5 (–7) mm long, occasionally with a few villous hairs toward the base; stigma cream, clavate, 1.1–2 mm long, 0.7–1.2 mm thick, occasionally exerted beyond the longer stamens. Capsules erect, sparsely strigillose, 2.5–4.2 cm long, 1.5–2 mm thick on pedicels 0.6–1.7(–2.5) cm long. Seeds brown, papillose, obovoid, 1.4–1.9 mm long, 0.5–0.65 mm thick; coma white to slightly yellowish, 4–7 mm long.

Distribution (Fig. 8): On rocky, stable scree, or rocky stream banks, near or above timberline, or extending to lower elevations along gravelly stream beds, or on volcanic cinders. Central Andes of Chile and Argentina, from Paso Portillo (33°S), southward along the mountains to the vicinity of Lago Puelo, Chubut Prov., Argentina, usually between 1,200–2,700 m, rarely as low as 800 m. Flowering late December to early March.

Specimens examined: ARGENTINA, CHUBUT: Lago Puelo, *Pérez-Moreau in 1941* (BA, RSA). NEUQUÉN: Parque Nacional Nahuel Huapi, Refugio Cerro Colorado, *Boelcke 6900* (BAA, BAB, MO), *de la Sota 2245* (LIL); Parque Nacional Nahuel Huapi, filo entre Cerro Angostura y Cerro Mojón, *Boelcke & Correa 7115* (BAA, BAB); Dpto. Minas, Paso del Macho, 2,280 m, 36°26'S, 70°46'W, *Boelcke et al. 13905* (BAA, BAB, MO), *13915* (BAA, BAB, MO); Dpto. Lácar, Cerro Chapelco, 40°14'S, 71°16'W, *Cabrera 20532* (LP), *Correa et al. 5908* (BAB); Parque Nacional Lanín, Arroyo Rucu-leufú, *Correa et al. 5663* (BAB, MO); Ridge to Mt. O'Connor, *Diem 3600* (MO); Parque Nacional Lanín, Cerro Malo, *Dimitri et al. in 1963* (BAB), *León & Calderon 1328* (BAA, MO); *Schajovskoy in 1968* (LP); Faldeos del Volcán Lanín, 1,600 m, *Gentili 533* (CTES); Lago Nahuel Huapi, Río Huemul, 770 m, *Ljunger 766* (GB); Lago Nahuel Huapi, Cordón del Colorado, Cerro de la Curva, *Pérez-Moreau in 1940* (BA, MO, RSA). RÍO NEGRO: Cerro Tronador, *Cabrera & Crisci 19231* (LP); *Castagnet 83* (LP), *Dimitri et al. in 1964* (BAB), *Gentili in 1975* (MO), *Maldonado 261* (GH, LP); *Solomon 4638* (MO); Cerro V. López, W of Bariloche, *Fabris 2177* (M), *Solomon 4618* (MO); Cerro Catedral, *Fabris 2233* (LP, M); Cerro Goye, 41°07'S, 71°30'W, *Hosseus 263* (CORD); Parque Nacional Nahuel Huapi, Cerro Riggi, *Marchionni 222* (LP); Lago Frías, camino al Ventisquero Frías, *Montiel in 1946* (LIL), *Pérez-Moreau in 1940* (BA, MO, RSA); E side of Lago Guillermo, 810 m, 41°25'S, 71°28'W, *Solomon 4645* (MO); Parque Nacional Nahuel Huapi, nacimiento del Río Manso, *Vervoorst in 1948* (LIL).

CHILE, V REGIÓN (ACONCAGUA): *Los Andes*, Paso Portillo, 2,700 m, *Wall in 1946* (GB, S). VI REGIÓN (O'HIGGINS): *Cachapoal*, Hacienda de Cauquenes, *Dessauer in 1875* (M); Ventisquero Cipreses, *Dessauer in 1876* (SGO). VII REGIÓN (MAULE): *Curicó*, Las Yeguas, 35°23'S, 70°30'W, *Borchers in 1880* (GOET); Lagunas de Teno, 2,550 m, 35°12'S, 70°30'W, *Mahu 5682* (H); Volcán Peteroa, *Philippi (?) in 1896* (BM). VII REGIÓN (BÍO-BÍO): *Bío-Bío*, Laguna La Laja, *Boelcke et al. in 1969* (BAA, BAB, CTES), *Cabrera 19675* (LP); *Clark & Brown 1393* (ASU, MO); *Solomon 4433* (MO);

Zöllner 6225 (MO, NA), 9370 (MO); Cordillera Araucanía, La Cueva, *Rahmer in 1886* (JE, SGO); Trapa-Trapa, *Rahmer in 1886* (SGO). Ñuble, Termas de Chillán, *Jaffuel 2794* (GH), *Pennell 12429* (F, GH, NY, PH, S, US), *Pfister in 1947* (CONC), *Ricardi 5588* (MO). IX REGIÓN (ARAUCANÍA): Without precise locality, *Philippi in 1888* (CORD, K, US, WU). Malleco, Termas del Río Blanco, 1,200 m, *Clark & Brown 1407* (ASU, MO), *Klempau in 1972* (VALD), *Montero 3675* (GH), *Pfister in 1948* (CONC); *Solomon 4495* (MO); 4504 (MO); 4506 (MO); Termas de Tolguaca, *Pfister in 1939* (CONC); Volcán Lonquimay, 1,600 m, *Sparre & Constance 10909* (CONC, UC); Paso Lolco, 1,500 m, *Zöllner 6245* (MO); 10209 (MO).

Epilobium densifolium is a strikingly handsome plant with large pink or rose purple flowers, small lanceolate leaves, caespitose habit, and a contorted, often woody rootstock. Some individuals of *E. densifolium* might possibly be confused with smaller leaved plants of *E. australe*, although they can be readily distinguished by the few large flowers, seeds longer than 1.4 mm, and the stem pubescence distributed around the stems throughout.

Epilobium densifolium was described from a single Poeppig collection seen by Haussknecht at Leningrad (LE). Part of the Leningrad material was separated by Haussknecht for his herbarium, now at Jena (JE), and a fragment of that was acquired by Samuelsson, who saw only Haussknecht's specimens. Samuelsson (1923) maintained *E. densifolium* as distinct from *E. pauciflorum* R. Phil. and went so far as to include it in the group Palustriformia, along with *E. puberulum*, based on the lack of raised decurrent lines from the petiole margins. A close examination of the available type specimens, however, shows that there are evident raised lines in the upper portions of the stems. The flowers and seeds of the type are smaller than is typical for the species, but all other morphological features can be easily included in the species as it is circumscribed here.

The name *Epilobium pauciflorum* was proposed only a few years later (Philippi, 1893) for two collections of large-flowered plants from Araucanía, but this name proves to be a later homonym. R. Philippi stated in the description "E. suffruticosum, glaberrimum, humile;" The specimens cited, however, are not glabrous, but more or less densely strigillose. There is no confusion as to which specimens Philippi was describing from his annotations, so this must have been an accidental error. Most collections have been identified as *E. pauciflorum* primarily because of the uncertain identity and relationship of the type of *E. densifolium*.

Epilobium densifolium occurs in the driest sorts of habitats of any native South American *Epilobium* species, growing in rocky scree, often along stream banks, but frequently on hillsides, and not necessarily associated with running water. In one instance, a large population was found growing in dry, loose cinder scree on the lower slopes of Volcán Antuco (*Solomon 4433*, MO). These plants had the longest, woodiest roots of any collection seen, up to 30 cm long and 5 mm thick.

Of the native species in South America, *E. densifolium* produces the largest flowers and seeds. Only a few populations or individuals of *E. denticulatum* and *E. australe* have flowers that overlap with the lower portion of the size range for *E. densifolium*. Petal color varies from pink to rose purple, often with the distal end of the petal having the darkest shade, fading to white at the proximal end.

Normally at anthesis the anthers are held away from the stigma. Some hours after the flowers open, the longest stamens bend inward and the anthers usually make contact with the lower portion of the clavate stigma. Only rarely is the

stigma fully exerted beyond the longest stamens (Paso Lolco, Prov. Malleco, Chile, Zöllner 6245, MO). The result is that in most populations, if the flower is not cross-pollinated, at least some measure of self-pollination will occur.

Because of these features one might expect that hybrids involving *E. densifolium* and other species might be fairly common. This does not appear, however, to be the case, even though *E. densifolium* grows sympatrically with four other species. Only a few collections show intermediate morphological characters that would indicate hybridization in their ancestry, with *E. glaucum* most likely as the other parent. For example, *Dimitri et al. in 1964* (BAB) from Monte Tronador, Río Negro Prov., Argentina, and *Solomon 4495* (MO) from Termas del Río Blanco, Malleco Prov., Chile, both show the long, narrowly acuminate, sparsely toothed leaves of *E. glaucum*, are much more robust and less leafy than is typical for *E. densifolium*, but in other characters are more *E. densifolium*-like. Two other collections, *Solomon 4433* (MO) and *Clark & Brown 1393* (MO), both from populations along the lower slopes of Volcán Antuco, Bío-Bío Prov., Chile, show particularly strong indications of hybrid origin between *E. densifolium* and *E. glaucum*, with reduced pollen stainability (54% and 61%, respectively), as well as intermediate habit and leaf morphology.

Epilobium australe may also be involved in hybridization with *E. densifolium*, but hybrids would probably be difficult to distinguish. One such possible hybrid comes from Volcán Osorno, Osorno Prov., Chile (*Sparre & Constance 10722*, CONC). This collection has the thick, woody rhizomes of *E. densifolium*, the leaves intermediate between the two species, but the narrower capsules and smaller seeds of *E. australe*. Specimens of *E. densifolium* have not been seen from Volcán Osorno, but it does occur within 40 km, while *E. australe* is represented by a number of collections from this area. This odd collection may be only an unusual form of *E. australe*, but it is very unlike any other specimens seen, which suggests a possible hybrid origin.

9. ***Epilobium australe*** Poeppig & Hausskn. ex Hausskn., Monogr. *Epilobium* 269. 1884. TYPE: Chile, VIII Región (Bío-Bío), Prov. Bío-Bío, Volcán Antuco, February 1829, *E. Poeppig* (W, lectotype here designated, photographs GH, MO; OXF, isoelectotype; BR, JE, M, P (photograph GH), PR, W, probable isoelectotypes). Reiche, Fl. Chile 2:247. 1898. H. Lév., Iconogr. *Epilobium*, tab. 209. 1911. Samuelsson, Svensk Bot. Tidskr. 17:282. 1923; Svensk Bot. Tidskr. 24: 4. 1930.

E. tetragonum β *antarcticum* Hook. f., Fl. Antarct. 2:270. 1847. *E. antarcticum* (Hook. f.) Kuntze, Rev. Gen. 3(2):97. 1898. TYPE: Chile, XII Región (Magallanes), Prov. Magallanes, Puerto del Hambre (Port Famine), 53°38'S, 70°56'W, 1827, *P. King* (Commander of the first voyage of the *Adventure & Beagle*) (K, lectotype here designated, photograph MO; BM 2 sheets, E, K, isoelectotypes).

E. lechleri R. Phil. & Hausskn. ex Hausskn., Monogr. *Epilobium* 270. 1884. *E. australe* var. *lechleri* (R. Phil. & Hausskn. ex Hausskn.) Samuelsson, Svensk Bot. Tidskr. 17:285. 1923. TYPE: Chile, XII Región (Magallanes), without specific locality, 1865(?), *R. A. Philippi* (W, lectotype here designated, photograph MO; W 2 sheets, isoelectotypes; B (destroyed, photographs BH, GH, MO, NA, NY), SGO-53103 (photograph MO), UPS, probable isoelectotypes). The date is taken from SGO-53103, which matches the 3 specimens at W in all morphological particulars. Reiche, Fl. Chile 2:248. 1898.

E. lechleri var. *antarcticum* Macloskie, Rep. Princeton Univ. Exped. Patagonia 8(5):609. 1905, non Hausskn., Monogr. *Epilobium* 270. 1884. *E. lechleri* var. *antarcticum* Hausskn. ex Macloskie &

Dusén, Rep. Princeton Univ. Exped. Patagonia, Revision Fl. Patagonica 185. 1914, nom. superfl. TYPE: Chile, XII Región (Magallanes), Prov. Antártica Chilena, Isla Hoste, Orange Harbour, *without date or collector* (presumably collected by the U.S. Exploring Expedition under the command of Charles Wilkes, because these are the only Orange Harbour collections known, February–March 1839). The description and locality information are apparently copies in shortened form from Haussknecht (1884), although Macloskie may have seen specimens at NY where he did some of the work on the *Report*. Since there is no direct or indirect reference to Haussknecht's work at the time of publication, this must be considered a new name. Later Macloskie & Dusén (1914) referred this name to *E. lechleri* var. *antarcticum* Hausskn.

E. australe var. *pumilum* Samuelsson, Svensk Bot. Tidskr. 17:28. 1923. TYPE: Chile, XII Región (Magallanes), Prov. Tierra del Fuego, Sierra Valdivieso, near Paso de Las Lagunas, 800 m, 11 March 1908, C. Skottsberg 232b (UPS, lectotype here designated, photograph MO).

E. australe var. *andinum* (R. Phil.) Samuelsson, Svensk Bot. Tidskr. 17:284. 1923. Based on *E. andinum* R. Phil., pro parte. The new combination was based on a Philippi collection at B (destroyed), presumably a specimen of *E. australe* annotated by Philippi as *E. andinum*. Samuelsson's assignment of this specimen as a variety of *E. australe* is probably reliable, since his understanding of *E. australe* was accurate, as indicated by his exsiccatae. I have seen R. Philippi's handwritten annotations of '*E. andinum*' on collections of three different species, *E. ciliatum* subsp. *ciliatum*, *E. australe*, and *E. nivale*. The epithet, *E. andinum*, is most correctly assigned as a synonym of *E. nivale* (q.v. for a discussion of this nomenclatural problem).

E. deflexum Samuelsson, Svensk Bot. Tidskr. 17:286, tab. 5, f. 1. 1923. TYPE: Chile, XII Región (Magallanes), Prov. Magallanes, banks of Río de Las Minas (Punta Arenas), 16 February 1908, C. Skottsberg 232 (UPS, lectotype here designated, photographs MO, S; S, isolectotype).

E. interruptum Samuelsson, Svensk Bot. Tidskr. 17:286, tab. 3, f. 3. 1923. *E. australe* var. *interruptum* (Samuelsson) Samuelsson, Svensk Bot. Tidskr. 24:8. 1930. TYPE: Argentina, Prov. Chubut, cerca Lago General Paz, 27 January 1901, G. Gerling 210 (C, lectotype here designated, photographs MO, S; BAF, UPS, Z, isolectotypes).

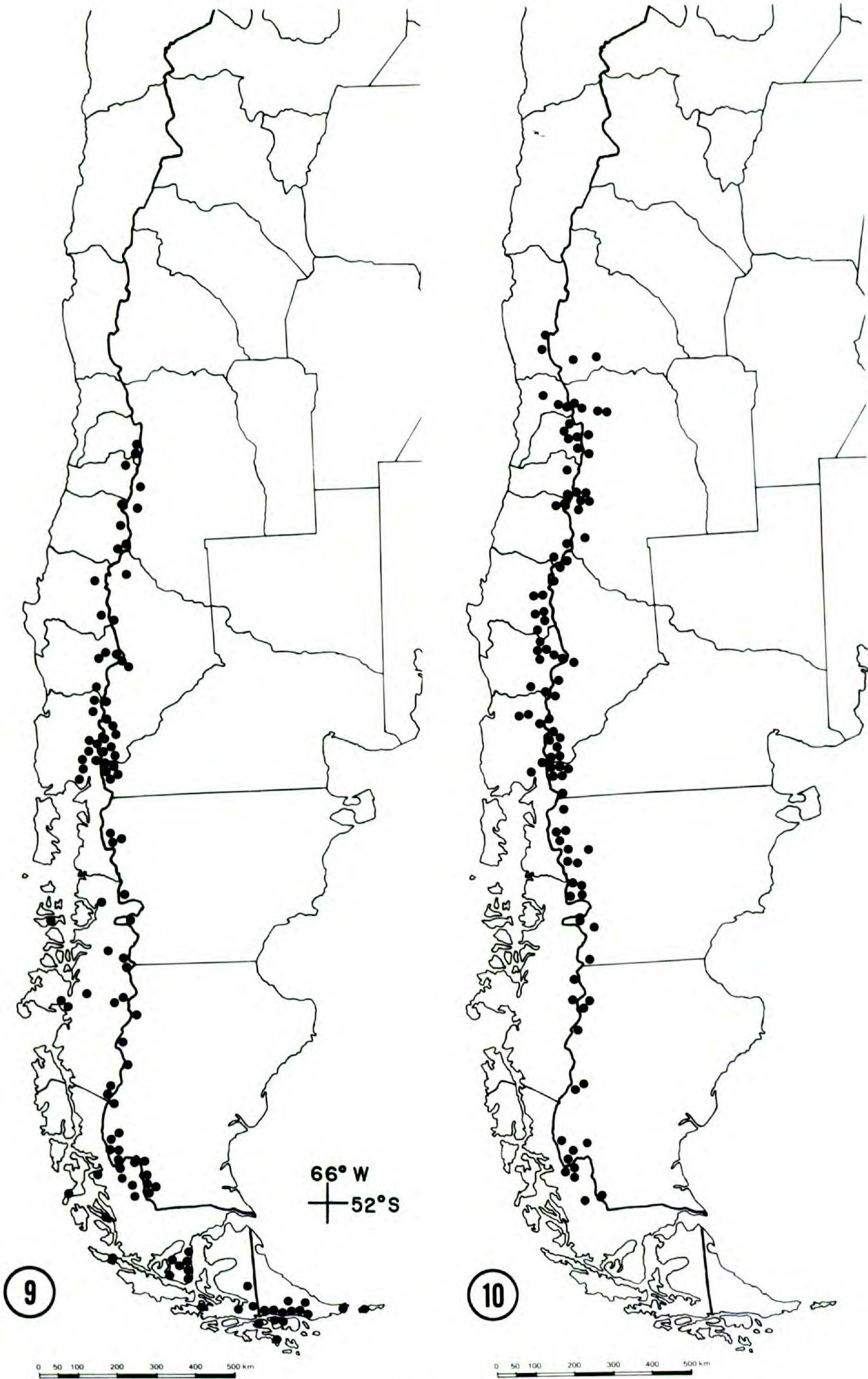
E. transandinum Samuelsson, Svensk Bot. Tidskr. 17:287, tab. 4, f. 6. 1923. TYPE: Argentina, Prov. Santa Cruz, Lago Viedma, "in uliginosis," 22 February 1905, P. dusén 5883 (UPS, lectotype here designated, photographs MO, S; B (destroyed, photographs BH, MO, US), BAF, K, W, isolectotypes).

Clumped perennial herbs, (5–)15–35(–50) cm tall, overwintering and reproducing vegetatively by short rhizomes terminated by leafy shoots or soboles. Rhizome with scale-like leaves, 2–5 mm long, 1–2 mm wide. Stems ascendent, simple, branching generally only from the base, occasionally above, terete, often reddish purple, strigillose, the hairs 0.1–0.2 mm long, in raised descending lines from the decurrent petiole bases, or scattered thinly over the stem surface. Leaves mostly opposite, alternate only in the inflorescence, thick, dull green, often purplish, especially on the margins, narrowly ovate to ovate, rarely broadly so, (0.6–)1–3(–4) cm long, (0.3–)0.6–1.4(–2.2) cm wide, acute to acuminate, rarely obtuse at the apex, remotely, irregularly and coarsely serrate with 4–8(–12) teeth on each side, acute to cuneate, or occasionally rounded to subcordate at the base, strigillose on the adaxial midrib or the upper surface, the lower surface glabrous, the lateral veins prominent, 2–3(–4) on each side of the midrib, on petioles 0–2 mm long. Inflorescence erect, simple. Flowers erect. Ovaries usually reddish purple, strigillose, occasionally densely so, 0.8–1.4 cm long, on pedicels 0–3 mm long. Floral tube reddish purple, 0.4–1.3 mm deep, 1.5–2.7(–3.5) mm across, externally strigillose, internally with a conspicuous ring of erect villous hairs 0.1–0.13 mm long near the base. Sepals often reddish purple, lanceolate, 2.5–4.1 mm long, 1.2–1.7(–2.1) mm wide, slightly keeled at the base, with scattered strigillose hairs along the margins. Petals pale pink, obovate, rarely broadly so, 4–6.2(–9.2) mm long, 2.6–4.5(–7) mm wide, the notch 0.8–1.6(–3.3) mm deep. Anthers cream to white, 0.5–0.8 mm long, 0.3–0.7 mm wide; filaments cream to white, those of the longer stamens 1.5–2.5 mm long, those of the shorter 0.8–1.6 mm long; the

anthers usually held away from the stigma at anthesis, but the longer stamens, and occasionally the shorter, bending and shedding on the stigma after anthesis. Style cream to white, 1.3–3 mm long; stigma cream to white, clavate to capitate, 0.7–1.5(–1.8) mm long, 0.4–1 mm thick. Capsules erect, occasionally deflexed before dehiscence, with scattered strigillose hairs, occasionally glabrous, 3–5 cm long, 1.2–1.7 mm thick, on pedicels 0.3–2.5(–3) cm long. Seeds brown, papillose, obovoid, 1–1.4 mm long, 0.4–0.5 mm thick; coma white to slightly yellowish, 4–7 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 9): Usually inhabiting moist sand or gravel, or growing between rocks along streams or seeps, almost always in or near permanently flowing water. Widely distributed throughout the central and southern Andes of Chile and Argentina, from the upper Valle del Maipo (Cordillera Prov., Chile; 34°S) southward along the mountains to southernmost Tierra del Fuego. In the north, ranging from 2,000–3,700 m, gradually descending southwards to between sea level and 700 m in southern Patagonia and Tierra del Fuego. Flowering (December) January to March.

Representative specimens examined: ARGENTINA, CHUBUT: Dpto. Futaleufú, Esquel, La Hoya, 1,600 m, *Cabrera 23176* (CTES, LP); Dpto. Futaleufú, Lago Futalaufquén, *Soriano 4170* (BAA, MO); Parque Nacional Los Alerces, Lago Verde, *Soriano 4212* (BAA, MO); Lago La Plata, Río Unión, 44°53'S, 71°50'W, *Yplesias & Soetbeer in 1969* (LP). MENDOZA: Antes de llegar al Indigeno, Volcán Overo, 3,700 m, *Lagiglia 2231* (LP); Dpto. Malargüe, Valle Hermoso, *Stuckert 3081* (CORD, mixed with *E. ciliatum*). NEUQUÉN: Cerro Colorado, entre Pto. Manzano y Lago Traful, *Boelcke & Correa 6932* (BAA, BAB); Dpto. Chos Malal, Arroyo de Los Tábanos, 2,330 m, 36°44'S, 70°25'W, *Boelcke et al. 11342* (BAA, MO); San Martín de Los Andes, *S. T. de Burkhart in 1976* (SI); Arroyo Las Lajas, 1,500 m, 38°47'S, 70°42'W, *Comber 287* (E); Dpto. Huiliches, Volcán Lanín, Arroyo Rucu-leufú, *Correa et al. 5596* (BAB, mixed with *E. ciliatum*); Dpto. Lácar, Cerro Chapelco, *Crespo & Giangualani 2079* (BAB, MO); Pino Hachado, *Dawson & Schwabe 2229* (BAA, BAB); Laguna Trolope, 1,700 m, *DeBarba 2017* (BAA, LIL); Paso Puyehue, 1,500 m, *Diem 3604* (MO); Dpto. Lácar, Cerro Malo, 1,700 m, *Hunziker 7006* (BAB); Lago Nahuel Huapi, Río Huemul, 770 m, *Ljungner 765* (GB, MO); Lago Nahuel Huapi, Brazo Rincón, Cerro Dormilón, *Pérez-Moreau in 1940* (BA, LIL, MO, RSA); Volcán Copahue, *Pérez-Moreau in 1941* (BA, MO, RSA); Lago Nahuel Huapi, valle Río Machete, 40°48'S, 71°45'W, *Pérez-Moreau in 1943* (BA, RSA); Parque Nacional Nahuel Huapi, Laguna Frias, *Boelcke & Correa 5372* (BAA, BAB, SI). RÍO NEGRO: Cerro Tronador, entre Mallín Chileno y Refugio, *Boelcke & Correa 5738* (BAA, BAB, SI); Cerro López, 1,700 m, W of Bariloche, *Burkhart 6160* (BA, F, GH, MO, RSA); Cerro Catedral, SW of Bariloche, 1,850 m, *Crespo & Giangualani 2097* (BAB, MO); Parque Nacional Nahuel Huapi, Laguna Los Clavos, *Pedersen 271* (BR, C, P, S, US); Cerro Tronador, *Rubulis in 1976* (MO); Río Llogdconto, 41°22'S, 71°30'W, *Solomon 4629* (MO). SANTA CRUZ: Lago Argentino, Ventisquero Upsala, Cerro Cono, 900 m, *Adam in 1953* (LIL, US); Lago Argentino, Estancia Lago Roca, Cerro Fraile, 760 m, *James 428* (BM, DS, SI); Laguna Fría, 500 m, 50°42'S, 73°03'W, *James 831* (BM, DS); Cerro Mayo, 800 m, 50°22'S, 73°18'W, *James 5036* (BM, DS); Sierra Sangra, Río El Capón, 1,600 m, 48°22'S, 72°21'W, *Kraftsik in 1968* (BAB); Lago de Los Tres, Cerro Fitz Roy, *Luti in 1957* (CORD); Entre Río Geo y Lago Pueyrredón, 600 m, *von Platen & Greiner 121* (BAF, SI, MO, Z); Lago Burmeister, 800 m, *von Platen & Greiner 122* (BAF, SI, MO, Z); Dpto. Argentino, Glaciar Perito Moreno, 190 m, 50°28'S, 73°02'W, *Solomon 4659* (MO); Dpto. Güer Aike, Estancia Achalay, 50°55'S, 72°12'W, *T.B.P.A. (Arroyo et al.) 2349* (HIP, MO, RNG); Dpto. Güer Aike, Estancia Stag River, 410 m, 51°38'S, 71°57'W, *T.B.P.A. (Boelcke et al.) 3132* (BAB, MO); Dpto. Güer Aike, curso superior del Río Turbio, 51°28'S, 72°05'W, *T.B.P.A. (Roig et al.) 3145* (BAB); Dpto. Güer Aike, Estancia La Primavera, 430 m, 51°36'S, 72°17'W, *T.B.P.A. (Ambrosetti & Mendez) 4092* (MO, mixed with *E. ciliatum*); Dpto. Lago Argentino, Lago Viedma, *Witte 24* (BA, BAF, NY, SI). TIERRA DEL FUEGO: Bahía Buen Suceso, 54°47'S, 65°15'W, *Banks & Solander in 1769* (BM, GH, S, US); Almanza, 54°53'S, 67°37'W, *Castellanos in 1932* (BA, MO, RSA); Isla de Los Estados, Bahía Liberty, 54°49'30"S, 64°26'W, *Dudley et al. 1274* (E, MO, RNG, SGO, UC); Near Paso Garibaldi, 330 m, *Goodall 601* (MICH, NA, P, RNG, RSA, UC, US); Estancia Punta Segunda, Río Punta Segunda, *Goodall 1968* (LTR, MICH, MU, NA, UC); Estancia La Correntina near No Kake Mtn., *Goodall 2011* (NA, RNG); Lapataia, edge of Lago Roca, *Goodall 2434* (BAB, NA, RNG); Estancia Cullen, Pampa de Beta, *Goodall 2547* (RNG); Estancia Moat, Río Moat, 54°56'S,



FIGURES 9-10. Distribution of *Epilobium* species.—9. *E. australe*.—10. *E. glaucum*.

66°44'W, *Moore* 1686 (MO); Monte Spion-Kop, 54°44'S, 67°18'W, *Moore* 2803 (MO); Ushuaia, Arroyo Buena Esperanza, 130 m, *Solomon* 4747 (MO).

CHILE, REGIÓN METROPOLITANA (SANTIAGO): *Cordillera*, Valle del Yeso, *Gerling* 6088 (BAB, MO; mixed with *E. glaucum*); Los Paramillos, Valle del Maipo, 3,750 m, *Grandjot* 3768 (SI, mixed with *E. glaucum*). VI REGIÓN (O'HIGGINS): *Cachapoal*, Río Coya, above El Teniente, 2,900 m, *Pennell* 12321 (F, GH, NY, PH, S, SGO, US). VII REGIÓN (MAULE): *Curicó*, Volcán Peteroa, 2,000 m, *Werdermann* 599 (BM, CAS, E, F, G, GH, LIL, MO, NY, S, U, UC, US, Z). *Linares*, Cordillera de Linares near Laguna Maule, 2,200 m, *Schlegel* 3508 (LA). *Talca*, Laguna del Maule, 2,200 m, *Parra & Rodríguez* 189 (CONC). VIII REGIÓN (BÍO-BÍO): *Bío-Bío*, La Cueva, *Rahmer in 1887* (SGO); Laguna La Laja, 930 m, 37°25'S, 71°25'W, *Solomon* 4441 (MO). *Ñuble*, Termas de Chillán, 2,100 m, *Pennell* 12437 (F, GH, NY, PH, S, SGO, US), 2,200 m, *Werdermann* 1314 (BM, CAS, F, G, GH, LIL, MO, SI, U; mixed with *E. ciliatum*). IX REGIÓN (ARAUCANÍA): *Cautín*, Parque Nacional Conguillio, 38°39'S, 71°38'W, *Martcorena et al.* 834 (CONC); Volcán Villarrica, entre el Refugio y Pucón, 650 m, *Rojas in 1948* (SGO); Volcán Llaima, 1,350 m, 38°43'S, 71°43'W, *Solomon* 4514 (MO). *Malleco*, Paso Pino Hachado, *Merxmüller* 25013 (M); Termas del Río Blanco, 1,300 m, 38°35'S, 71°35'W, *Solomon* 4498 (MO). X REGIÓN (LOS LAGOS): *Llanquihue*, Puerto Montt, Pangal, without collector in 1958 (VALD); Cerro Vichadero-Casa Pangué, 1,500 m, 41°05'S, 71°51'W, *Pfister in 1953* (CONC); Volcán Calbuco, Río Aguas Calientes, 41°20'S, 72°37'W, *Rudolph in 1943* (VALD). *Osorno*, Azufreras Volcán Puyehue, 1,350 m, *Rudolph in 1941* (VALD); Volcán Casablanca, Antillanca, 1,000 m, 40°45'S, 72°12'W, *Solomon* 4576 (MO); Lago Constanza, 1,000 m, 40°38'S, 71°54'W, *Sparre & Smith* 353 (CONC, mixed with *E. ciliatum*). *Valdivia*, Camino de Coñaripe a Puerto Fui, Km 6, *Martcorena et al.* 475 (CONC); Volcán Choshuenco, *Moore* 344 (LA). XI REGIÓN (AISEN) *Aisen*, Chonos Archipelago, *Darwin in 1834* (K); Istmo de Ofqui, *Hicken in 1921* (LIL, SI); Golfo San Estebán, Ventisquero San Quentín, 80 m, 46°55'S, 74°05'W, *Hoppe* 11 (RNG); E of Puerto Aisen, *Pirion* 3394 (GH); Puerto Puyuhuapi, Cerro Tesoro, 900 m, 44°21'S, 72°34'W, *Schwabe* 82 (CONC, NY). *Gral. Carrera*, Río Jeinemeni, 30 km S of Lago Buenos Aires, 880 m, *Grosse* 23 (CONC, NY); Río Exploradores, Ventisquero Circo, 150 m, 46°20'S, 73°15'W, *Seki* 196 (CONC); Lago Buenos Aires, Cerro Pirámide, 1,200 m, *Zöllner* 7730 (MO). *Coihaique*, Portezuelo, 800 m, *Behn in 1934* (CONC); Balmaceda, 580 m, *Maldonado* 155 (LP). *Capitán Prat*, Península Florida, 1,300 m, 48°40'S, 73°40'W, *Donat* 548 (G); Lago San Martín, Estación Ramona, 900 m, *Grosse* 56 (LIL, S). XII REGIÓN (MAGALLANES): *Antártica Chilena*, Seno Ponsonby, 220 m, 55°05'S, 68°58'W, *Adams & Andrews-Speed* 21 (HIP, RNG); West end of Isla Navarino, *Hicken* 62 (BAF); Isla Navarino, NW of Puerto Williams, 400 m, *Moore* 359 (LA); Orange Harbour, 55°31'S, 68°03'W, *Wilkes (U.S. Exploring Expedition) in 1839* (K, MO, NY, P, US, JE fragment). *Magallanes*, Puerto Charruca, 53°02'S, 73°56'W, without collector or date (E); Seno Otway, Río Caleta, *Cárdenas* 21 (HIP, MO); Near Punta Arenas, Cerro Mirador, 670 m, *Dollenz* 152 (HIP, MO); Tres Puentes, 200 m, 53°07'S, 70°53'W, *Donat* 305 (BA, BAF, BM, CAS, F, GH, K, M, NY, SI, U, Z); 15 km S of Punta Arenas, *Eyerdam et al.* 24111 (G, MICH, MO, NA, S, SI, UC, WTU); Cerro Tar, Faro San Isidro, 53°48'S, 70°55'W, *Hernandez* 3 (HIP); Port Gallant, 53°40'S, 71°58'W, *Jacquinet in 1841* (P); Punta Arenas, Chabunco, *Magens in 1951* (CONC); Laguna Parrillar, 53°25'S, 71°17'W, *Pisano* 3925 (HIP, MO, RNG). *Tierra del Fuego*, Glaciar Reina Isabel II, 54°31'S, 69°15'W, *Pisano* 3021 (HIP, MO, RNG); Vicuña, *Ricardi & Matthei* 226 (CONC); Fjordo Almirante Martínez, Seno Plüschow, 54°27'S, 70°40'W, *Roivainen in 1929* (BA). *Última Esperanza*, Isla Diego de Almagro, Puerto Pelantaro, 51°24'S, 75°04'W, *Biese* 1465 (LIL, SGO); Cerro Prat, 51°29'S, 72°47'W, *Fester in 1931* (SI); Cerro Toro, Sección Lazo, 51°10'S, 72°45'W, *Pisano* 4104 (HIP, MO); Estancia La Cumbre, Sierra Baguales, 50°36'S, 72°30'W, *Pisano & Cárdenas* 4685 (HIP, MO); Glaciar Grey, 51°00'S, 73°10'W, *Steele* 112 (RNG); Península Roca, Seno Resi, 750 m, 51°51'S, 73°02'W, *T.B.P.A. (Pisano)* 2923 (BAB, MO); Peel Inlet, 450 m, *Tilman* 63 (BM); 0.4 km W of Lago Paine, Río Paine, 150 m, *Williams in 1980* (MO, mixed with *E. glaucum*).

Epilobium australe is quite variable in the size of the plants and the density and size of leaves, but it is readily separable from the other species in South America. Plants usually have mostly opposite, thick, narrowly ovate to ovate leaves with few teeth, the stems first appearing as elongate leafy shoots from short scaly rhizomes, later ascendent, with strigillose pubescence. *Epilobium australe* is most likely to be confused with *E. ciliatum*, but the latter is easily distinguished by its turions, or compact leafy basal rosettes, thin lanceolate leaves with numerous teeth, and the presence of short glandular hairs in the inflorescence.

Plants referable to *Epilobium australe* were first collected by Banks and So-

lander from Tierra del Fuego in 1769. Although Solander gave them a manuscript name, *E. littorale*, the first published name did not appear until 1847 when Hooker described plants acquired by Captain King on the first voyage of the *Adventure* and *Beagle* as a variety of the common and variable European *E. tetragonum*. It was only with Haussknecht's revision of the genus that this distinctive species was given specific recognition (Haussknecht, 1884). Since then, numerous names have been proposed to cover the variations exhibited by *E. australe*, but none of them are distinct enough to warrant recognition based on current evidence, and a number were based on especially trivial characters. For example, *E. deflexum* was based on several plants with nodding inflorescences, a character that has not been seen in any other collections of *E. australe*. What seems most likely is that these plants were pressed in that position, perhaps after being carried through a day's hike in a dark vasculum. The curling of the growing inflorescences when carried in a dark place for some hours is very common; all species of *Epilobium* will do it. Similarly, *E. transandinum* was described because of its larger than average flowers, more rounded seeds and pubescent calyx lobes, all trivial characters when taken in context with the variability normally shown by *E. australe*.

The report of *Epilobium australe* from the Falkland Islands (Haussknecht, 1884) is probably due to a mixing of two separate collections. Three herbarium specimens, labeled as having been collected in the Falkland Islands (Antarctic Expedition, 1839–1843, J. D. Hooker, G, K, P), contain pieces of *E. australe* and *E. ciliatum*. The plants of *E. australe* are indistinguishable from those that compose the type material for *E. tetragonum* β *antarcticum* from Tierra del Fuego and were probably accidentally mixed with specimens of *E. ciliatum* from the Falklands when the material was distributed to other herbaria (cf. Skottsberg, 1913).

One of the most distinctive variants of this species is *Epilobium lechleri*. Haussknecht differentiated this from *E. australe* primarily on the basis of the more coarsely toothed, elongated leaves. These plants tend to be more robust, taller, with larger leaves than most other specimens. A formal taxonomic recognition for them, however, is not useful as plants of this type are found in populations throughout much of the range of *E. australe* and they intergrade continuously with the other plants in those populations. A fine example of this is the series of plants from Orange Harbour, Tierra del Fuego, Chile, collected on the U.S. Exploring Expedition, 1838–1842, in which the plants vary in size from 10 cm to about 40 cm, with small- and large-leaved individuals. Haussknecht identified two plants of the same size from this collection on the same herbarium sheet (K), one as *E. australe*, the other as *E. lechleri*, citing each in the respective protologue. The only differences between the two plants are that the one identified as *E. lechleri* is slightly more robust, with denser foliage composed of leaves with slightly larger teeth, and mature capsules.

There is some geographic basis for the variation seen in plant stature. Larger plants appear with greater frequency from the more southern portion of the species range, but equally large plants are also found much farther north. Superimposed on this geographical variation are elevational and microclimatic factors that also influence the size and leafiness of individual plants. Populations from higher el-

evations are often smaller and more densely leafy (e.g., Cerro Mayo, Santa Cruz Prov., Argentina, *James* 5036, BM, DS; Mt. Wood, Tierra del Fuego, Argentina, *Goodall* 3498, NA). Plants of this habit formed the basis for Samuelsson's *Epilobium australe* var. *pumilum*.

Similarly, exposure and moisture conditions have a profound effect on population variability. This is well illustrated by a series of collections from Volcán Llaima, Cautín Prov., Chile. Plants from a dry, sandy stream bed were low in stature (15 cm), well branched, and densely leafy, with mostly less than 1 cm leaves (*Solomon* 4513, MO); but plants found growing at the edges or in running streams were up to 35 cm tall, sparsely branched, with leaves mostly shorter than the internodes and over 2 cm long (*Solomon* 4514, 4516, 4517, 4519, MO). In addition, those from the drier and warmer sites had mature, dehiscent capsules, while those growing in the cold mountain streams were just beginning to flower. In the same manner, a population from Tierra del Fuego (*Solomon* 4747, MO) produced plants on a seep over rocks in full sun that were 15 to 20 cm tall with graceful stems and small leaves, while only a few meters away on a partially shaded gravel bar, robust plants over 50 cm tall, with large leaves, were common, along with numerous plants of intermediate size.

Ecologically *Epilobium australe* is found most often in rocky sites, especially seeps, or at the edge of rocky mountain streams where there is permanent flowing water, but it can occasionally be found on sand bars or at the edge of bogs. In these habitats it can grow sympatrically with up to five other *Epilobium* species, but only two, *E. ciliatum* and *E. glaucum*, and possibly a third, *E. densifolium*, are known to form hybrids with *E. australe*. Only those involving *E. glaucum* are presented here; the others are discussed under the other two species.

Epilobium australe and *E. glaucum* are broadly sympatric throughout much of their range, although *E. glaucum* extends farther north, while *E. australe* continues farther south. Often both species grow intermixed, and this close association makes occasional hybrids nearly inevitable. From the lower slopes of Volcán Llaima, Cautín Prov., Chile, several plants were collected (*Solomon* 4515, MO) that had intermediate morphology between the two species; glaucous, narrow leaves, and strigillose pubescence throughout. Pollen stainability of this collection was 34%. A second collection from Cerro López, Río Negro Prov., Argentina (*Cordini* 188, S) had similar morphology and poor capsule development.

10. ***Epilobium glaucum*** R. Phil., *Linnaea* 33:70. 1864, non Howell, Bull. Torrey Bot. Club 15:24. 1888. TYPE: Chile, Región Metropolitana (Santiago), Cordillera de Santiago, 1861, R. A. Philippi (K, lectotype here designated, photograph MO; G, probable isoelectotype). There is a specimen at SGO (53065) that bears two labels. One is in the hand of R. A. Philippi, with the annotation "*Epilobium glaucum* Ph.," from the Cordillera de Los Arañas, January 1861, collected by C. Landbeck. Attached below is a second label in the hand of C. Gay with the following information: "1222. Prov. Coquimbo in humidis andium huertado. Januario 1837." Because of the ambiguous nature of this sheet it has been excluded from consideration, and the lectotype chosen from the other specimens collected, and presumably annotated, prior to the date

of publication. Hausskn., Monogr. *Epilobium* 275. 1884. Reiche, Fl. Chile 2: 250. 1898. H. Lév., Iconogr. *Epilobium*, tab. 182. 1911. Samuelsson, Svensk Bot. Tidskr. 17:289. 1923. Dimitri, Región Bosques Andino-Patagonicos, tab. 63. 1972.

E. pedicellare auct. non Presl: Hook. & Arn., Bot. Misc. 3:309. 1833, pro parte.

E. mexicanum auct. non DC.: Walp., Nov. Act. Acad. Caes. Leopold. 19, Suppl. 1:328. 1843.

E. nubigenum R. Phil., Linnaea 33:71. 1864. TYPE: Chile, VIII Región (Bío-Bío), Prov. Ñuble, Baños de Chillán, 26 February 1862, R. A. Philippi. There is a mounted label on SGO-53071 in the hand of R. A. Philippi, but without an accompanying specimen, which bears the annotation "*Epilobium glaucum* var. *nubigenum* Ph." An additional annotation by C. Muñoz, February 1946 states, "Ejemplar extraviado, etiqueta junta a *E. glaucum* Ph." Reiche indicated that the specimens were lost at some point prior to his treatment of *Epilobium* in 1898 (Reiche, 1898). Based on the Latin description and the use of the epithet "*nubigenum*" as a variety of *E. glaucum* on the label, the placement of the name *E. nubigenum* as a synonym of *E. glaucum* is probably correct.

E. ramosum R. Phil., Anal. Univ. Chile 84:747. 1893, non Huds., Fl. Angl. 141. 1762. TYPE: Chile, VIII Región (Bío-Bío), Prov. Bío-Bío, Cordillera de Antuco, La Cueva, February 1887, C. Rahmer (SGO-41444, lectotype here designated, photographs GH, MO; SGO-53015, isoelectotype, photograph MO). H. Lév., Iconogr. *Epilobium*, tab. 195. 1911.

E. patagonicum Rendle, Journ. Bot. 42:367. 1904. TYPE: Argentina, Prov. Santa Cruz, Lago Argentino, Punta Bandera, lower slopes of Mt. Buenos Aires, February–March 1901, H. Prichard (BM, holotype, photograph MO).

E. glaucum var. *stenophyllum* Macloskie & Dusén, Rep. Princeton Univ. Exped. Patagonia, Revision Fl. Patagonica, Suppl. 185. 1914. TYPE: Argentina, Territory of Neuquén, northern Patagonia. No authentic material has been seen. Based on *E. glaucum* f. "*stenophylla*" Hausskn., Monogr. *Epilobium* 276. 1884.

Robust, loosely rhizomatous, perennial herbs, (15–)20–70(–100) cm tall, overwintering and reproducing vegetatively by scaly rhizomes terminated by elongate leafy shoots or soboles produced from near the base. Rhizome elongate, 5–20 cm long, with mostly opposite scale-like leaves, 2–6 mm long, 1–3 mm wide. Stems erect or ascendent, often clumped, simple, or sparingly branched above, to densely branched throughout, quadrangular or terete, reddish to purplish brown, glabrous, glaucous, with raised decurrent lines from the petiole bases. Leaves mostly opposite, alternate above or only in the inflorescence, rarely ternate, thick, green, glaucous, sometimes reddish, often with fascicles of small leaves in the axils, narrowly lanceolate, rarely broadly so, 1–4.1(–5) cm long, 0.2–1.2 cm wide, acuminate at the apex, remotely and coarsely denticulate with 2–7 teeth on each side, acuminate to cuneate, or acute, at the base, the lateral veins obscure, 1–3 on each side of the midrib, on poorly defined petioles 0–2 mm long. Inflorescence erect, simple, or occasionally branched, the floral leaves slightly if at all reduced. Flowers erect. Ovaries often reddish purple, glabrous, glaucous, 1.3–3.1 cm long, on pedicels 0.3–1(–1.5) cm long. Floral tube often reddish purple, glabrous, 0.8–1.9 mm deep, 1.5–2.1 mm across. Sepals often reddish purple, lanceolate, 3–5.2 mm long, 1–1.5 mm wide, glabrous. Petals pale pink, obovate, rarely broadly so, 4.2–7(–9) mm long, 2.4–4(–5) mm wide, the notch (0.7–)1.2–2.1 mm deep. Anthers cream to white, 0.9–1.1 mm long, 0.4–0.6 mm wide; filaments cream to white, those of the longer stamens 1.8–3.2 mm long, those of the shorter 1–1.7 mm long; usually the longer, and occasionally the shorter, stamens shedding directly on the stigma at or shortly after anthesis. Style cream to white, 3–4.9(–5.7) mm long; stigma cream to white, clavate, 0.9–1.9 mm long, 0.5–0.7 mm thick, rarely exserted beyond the anthers. Capsules erect, glabrous, 3.5–6 cm long, 1.2–1.6 mm thick,

on pedicels 0.5–1.8(–2.2) cm long. Seeds brown, papillose, obovoid, 1–1.3 mm long, 0.4–0.5 mm thick; coma white or slightly yellowish, 4.5–7 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 10): Common in moist sand, gravel, and among rocks along streams or seeps, embankments, roadsides, or other open, more or less permanently moist situations. Throughout the central and southern Andes of Chile and Argentina, from southern IV Región (Limarí Prov.), Chile, and San Juan Prov., Argentina, southward along the mountains to the vicinity of Torres del Paine and Puerto Natales, Chile. In the northern part of its range found typically from 1,900 to 3,000 m, descending gradually to 150–900 m at its southern limit. Flowering December to March.

Representative specimens examined: ARGENTINA, CHUBUT: Dpto. Cushamén, 30–40 km NE of Esquel, 42°49'S, 71°05'W, *Boelcke et al.* 16034 (BAA, BAB, MO); Los Rápidos, Río Futaleufú, *Castellanos in 1945* (BAB, F, LIL); Río Pico, 44°10'S, 71°18'W, *Fabiet in 1913* (BAB); Valle de Las Plumas, Lago General Paz, *Gerling 64* (BAF, Z); Río Pico, *Gerling in 1903* (SI); Región del Lago General Pico, 650 m, 44°05'S, 70°55'W, *Hazbera in 1902* (BAB, S, SI); Cholila, *Illin 129* (BAF, BR, CORD, SI); Carrenleufú, 43°50'S, 72°59'W, *Illin in 1900* (LP); Arroyo del Gato, Lago Fontana, 44°56'S, 71°30'W, *Koslowsky in 1896* (LP); Valle de la Laguna Blanca, 45°52'S, 71°15'W, *Koslowsky 80* (CORD, LIL, SI, Z); Camino de Corcovado a Tecka, *Krapovickas 4092* (BAB, LIL); Corintos, orillas del Río Corintos, 43°09'S, 71°35'W, *Lahitte in 1936* (BAB); Dpto. Lanquín, Arroyo Caquel, camino Tecka a Gobernador Costa, 43°22'S, 70°53'W, *Nicora 7510* (BAA, MO); Lago Epuyén, *Soriano 1375* (BAA, CTES, SI). MENDOZA: Dpto. Lujan, Chacras de Coria, 33°00'S, 68°52'W, *Araque 1240* (LIL); Dpto. Las Heras, Estación Polvoredas, 1,850 m, *Cuezzo & Balegno 1871* (LIL); Los Hoyos, 32°46'S, 69°23'W, *Gerth 98* (SI); San Rafael, Los Molles, *Kurtz 7551* (CORD, JE); Rincón de Los Arenales, entre el Paso de Portillo y La Laguna de Diamante, *Kurtz 10979* (CORD); Dpto. Malargüe, Valle Hermoso, 2,900 m, 35°08'S, 70°14'W, *Lagiglia 691* (LP); Dpto. Tunuyan, Valle del Alto Tunuyan, cerca Real de Contreras, *Leal 2124* (LIL, POM); Dpto. San Rafael, Río Grande, Minacar, 2,500 m, *Lourteg 7-94* (LIL, UC); Puente del Inca, *Malme 2935* (GH, LD, MO, S, UPS); Las Heras, Quebrada de Santa María, 2,600 m, 32°48'S, 69°51'W, *Palacios & Barkley 20MZ318* (NY, P, W); Dpto. San Rafael, Los Morros, *Rossi 296* (LIL); Valle del Atuel, Cajón del Burro, 2,700 m, *Wilczek 417* (G, US); Valle del Atuel, Arroyo Manga, *Wilczek 419* (G). NEUQUÉN: Confluencia Trafal, *DeBarba 2083* (LIL); Río Malleo, Lago Tromén, 1,000 m, 39°30'S, 71°22'W, *Böcher et al.* 1792 (DS); Dpto. Aluminé, Quillén, Estancia La Ofelia, *Boelcke 5174* (BAA, MO); Dpto. Minas, Laguna Epu-lauquén, 36°50'S, 71°07'W, *Boelcke et al.* 10908 (BAA, BAB, MO); Dpto. Minas, Valle del Río Pichi-Neuquén, puesto de Gendarmería, 36°36'S, 70°49'W, *Boelcke et al.* 13631 (BAA, BAB); Dpto. Minas, Laguna Varvarco Campos, Arroyo Benítez, 36°17'S, 70°39'W, *Boelcke et al.* 14200 (BAA, BAB, MO); Lago Huechulafquén, 39°46'S, 71°28'W, *Bridarolli 2109* (LP); Lago Nahuel Huapi, Brazo Blest, Arroyo Bravo, *Castellanos in 1938* (BA); Arroyo Las Lajitas, 38°31'S, 70°23'W, *Comber 295* (K); Lago Nahuel Huapi, Isla Victoria, *Cordini 79* (GH, S, US); Dpto. Lácar, Cerro Chapelco, 1,800 m, 40°14'S, 71°16'W, *Crespo & Giangualani 2074* (BAB, MO); Río Bonito, between Puerto Manzano and Villa La Angostura, 800 m, *Diem 3612* (MO); Dpto. Catán-Lil, Picunches, Cañón de Los Cipreses, 38°32'S, 70°15'W, *Kurtz 6322* (CORD, G, JE); Valle del Malalco, 39°15'S, 71°23'W, *Neger in 1891* (M); Lago Nahuel Huapi, Brazo Huemul, Arroyo Huelta, 40°58'S, 71°22'W, *Solomon 4628* (MO); Paso Pino Hachado, Refugio Militar Coronel Pringles, 1,400 m, *Valla et al.* 3092 (BAA, CTES, MO); Lago Nonthué, Arroyo Hua Hum, 40°09'S, 71°39'W, *Valla et al.* 3275 (BAA, CTES, MO). RÍO NEGRO: Arroyo Ñireco, 41°08'S, 71°17'W, *DeBarba 44* (A, LIL, NY, UC); Bariloche, 770 m, *Buchtien 1319* (BAF, BP, BREM, E, GH, L, M, PR, S, SI, W, Z); Parque Nacional Nahuel Huapi, Laguna Frías, *Cabrera 6072* (LP); El Bolsón, Río Quemquemtreu, *Correa et al.* 4191 (BAA, BAB, MO, UC); Villa Cerro Catedral, 1,030 m, 41°10'S, 71°28'W, *Solomon 4612* (MO); Cerro Tronador, 1,200 m, 41°10'S, 71°53'W, *Solomon 4641* (MO); South end of Lago Guillermo, 810 m, 41°25'S, 71°28'W, *Solomon 4643* (MO). SAN JUAN: Dpto. Calingasta, oeste de Barreal, El Pachón, 2,200 m, 31°38'S, 69°28'W, *Kiesling & Saenz 1467* (SI); Dpto. Calingasta, Cordillera de Espinazito, La Ciénaga Redonda, 31°40'S, 68°55'W, *Kurtz 9558* (CORD). SANTA CRUZ: Dpto. Lago Buenos Aires, 29 km NW of Perito Moreno, 46°25'S, 71°09'W, *Boelcke et al.* 16116 (BAA, BAB, MO); Lago San Martín at river, *Dusén 6081* (H, S, UPS); Dpto. Lago Argentino, 40 km W of Calafate, 270 m, *Eyerdam et al.* 24304 (G, GH, MO, NA, SI, UC); Dpto. Lago Argentino, S side of Lago San Martín, 340 m, *Eyerdam et al.* 24464 (G, GH, MO, NA, S, SI, UC); Dpto. Lago Argentino, Laguna Fría, 50°42'S, 73°03'W, *James 775* (BM, DS, SI); Entre Río Geo y Lago Pueyrredón, 600 m, *von Platen & Greiner 120* (BAF, MO, SI, Z); Los

Antiguos, 330 m, 46°35'S, 71°26'W, *Roivainen* 2585 (H); Dpto. Lago Argentino, Glaciar Perito Moreno, 190 m, 50°28'S, 73°02'W, *Solomon* 4657 (MO); Dpto. Güer Aike, Estancia La Primavera, 51°36'S, 72°17'W, *T.B.P.A. (Ambrosetti & Mendez)* 4086 (MO); Lago Argentino, Brazo Spegazzini, 50°15'S, 73°18'W, *Vervoorst* 4767 (LIL).

CHILE, IV REGIÓN (COQUIMBO): *Choapa*, Illapel, *Geisse in 1912* (Z). *Limari*, Vegas del Río Torca, 31°03'S, 70°43'W, *Geisse in 1890* (SGO); La Hierba Loca, 2,800 m, 31°25'S, 70°41'W, *Jiles* 4214 (CONC). V REGIÓN (ACONCAGUA): Los Andes: Valle del Río Blanco, *Boelcke* 2508 (BAA, CTES, MO); Juncal (Ojo de Agua), *Buchtien in 1903* (BAF, BM, BREM, E, L, M, S, SI, US, W), *Pennell* 12982 (F, GH, NY, PH, SGO, US), *Poeppig in 1830* (BM, F, G, HAL, MO, P, PR, W); Valle Monos de Agua, Refugio Mono Verde, *Schlegel* 2442 (CONC). *Petorca*, Cerro Chache, 18 km E of La Ligua, 1,900 m, *Morrison* 17042 (G, NA, UC). REGIÓN METROPOLITANA (SANTIAGO): *Cordillera*, Lo Valdes, Refugio Alemán, *Garaventa* 5678 (CONC); Cerro San Pedro Nolasco, 33°48'S, 70°16'W, *Gillies* (E, K); Los Paramillos, Valle del Maipo, 3,750 m, *Grandjot* 3768 (SI, mixed with *E. australe*); Valle del Yeso, entre Agua Panimávida y Agua Termal, 2,800 m, *Schlegel* 2580 (CONC). *Santiago*, Entre Maitenes y Pérez Caldera, 2,000 m, *Skottsberg & Sparre* 11062 (CONC, S); 2 km above Farellones, 2,650 m, 33°20'S, 70°18'W, *Solomon* 4356 (MO). VI REGIÓN (O'HIGGINS): *Cachapoal*, Hacienda de Cauquenes, *Dessauer in 1875* (M); Río Coya above El Teniente, 2,900 m, *Pennell* 12344 (F, GH, PH, SGO). *Colchagua*, Termas Vegas del Flaco, 1,750 m, *Mahu* 9855 (H, MO, UC). VII REGIÓN (MAULE): *Curicó*, Laguna de Teno, *Martcorena et al.* 7 (CONC, MO); 19 km al este de Los Queñes, 950 m, *Martcorena & Matthei* 798 (MO); Cordillera del Planchón, *Née in 1793* (MA, mixed with *E. ciliatum*). *Linares*, Termas de Longaví, *Castellanos in 1938* (BA). *Talca*, Laguna del Maule, 2,250 m, *Aravena* 1016 (UC); Cordillera de Maule, *Germain in 1856-57* (BM, G, K, P, W). VIII REGIÓN (BÍO-BÍO): *Bío-Bío*, Faldeo NW of Volcán Antuco, 1,350 m, *Boelcke et al.* 6384 (BAA, BAB); Al interior de Santa Barbara, 37°40'S, 72°02'W, *Gay* 1220 (SGO); Camino de Bío-Bío a Copahue, 5 km al este de Pitrillon, 840 m, *Martcorena et al.* 951 (CONC); Camino de Bío-Bío a Copahue, 4 km al este de Pitrillon, 770 m, 37°53'S, 71°31'W, *Martcorena et al.* 991 (CONC, MO); Baños de Pemehue, 38°03'S, 71°43'W, *Pinto in 1949* (CONC). *Ñuble*, Las Trancas, Purgatorio, 1,200 m, 36°48'S, 71°44'W, *Roivainen in 1929* (H); Termas de Chillán, 2,200 m, *Werdermann* 1312 (BM, CAS, E, F, G, GH, LIL, M, MO, NY, S, SI, UC, US, Z). IX REGIÓN (ARAUCANÍA): *Cautín*, Lonquimay, *Burkart* 9499 (LIL, SI); Volcán Lanín, *Claude-Joseph* 5539 (US); Volcán Llaima, 38°43'S, 71°43'W, *Solomon* 4518 (MO); Puente Correntoso, 15 km E of Villarrica, 210 m, 39°16'S, 72°00'W, *Solomon* 4537 (MO). *Malleco*, Termas de Tolguaca, 1,080 m, *Gunckel* 16362 (US); Buenavista, below Volcán Tolguaca, *Pennell* 12817 (F, GH, NY, PH, SGO); Túnel Las Raíces, boca Norte, 38°33'S, 71°30'W, *Pfister in 1947* (CONC); Termas del Río Blanco, 1,300 m, 38°35'S, 71°35'W, *Solomon* 4503 (MO); Volcán Lonquimay, *Sparre & Constance* 10928 (CONC, UC). X REGIÓN (LOS LAGOS): *Llanquihue*, Paso Pérez Rosales, 940 m, *Moore* 328 (LA, MO); Camino Ensenada a Ralun, *Pfister in 1948* (CONC). *Valdivia*, Daglipulli, 40°12'S, 72°59'W, *Gay* 79 (P); Lago Calafquén, *Martcorena et al.* 441 (CONC); Queñi, 40°15'S, 71°50'W, *Philippi(?) in 1887* (SGO); 1 km W of Coñaripe, 39°34'S, 72°00'W, *Solomon* 4539 (MO). XI REGIÓN (AISEN): *Aisén*, E of Puerto Aisén, *Pirión* 3413 (GH). *Gral. Carrera*, Cerro Pirámide, cerca Puerto Ibañez, *Zöllner* 7730 (NA). *Coihaique*, Río Coihaique, cerca puente hacia Los Leones, *Espinosa in 1934* (SGO); State Forest Manonegra, near Coihaique, *Schlegel* 6971 (VALD). XII REGIÓN (MAGALLANES): *Última Esperanza*, Eberhardt, 51°40'S, 72°38'W, *Borge* 138 (NY, S); Ventisquero Dickson, 50°48'S, 73°10'W, *Jenkins in 1977* (MO); Between Puesto Grey and Valle Olvidado, 50°56'S, 73°10'W, *Steele* 82 (RNG); Casas Viejas, 51°40'S, 72°20'W, *T.B.P.A. (Latour et al.)* 1814 (BAB, MO); 0.4 km W of Lago Paine on Río Paine, 130 m, *Williams in 1980* (MO, mixed with *E. australe*).

Epilobium glaucum is one of the most easily distinguished species in South America. The glabrous, glaucous, erect stems and long acuminate, few toothed leaves separate it immediately from all others. Only *E. nivale* is also glabrous, but it is characterized by a decumbent habit with small flowers and generally much smaller leaves.

There is relatively little variation in *Epilobium glaucum*. What does exist is most evident in the size of the leaves and branching pattern. As with many plants of open, sunny habitats, slightly shaded forms often have broader leaves and more lax, elongate stems; for example, *Solomon* 4641 (MO) from Monte Tronador, Río Negro Prov., Argentina. Also conspicuous are very narrow-leaved populations from Volcán Llaima (*Solomon* 4518, MO), although plants of this type are widely scattered throughout the range of the species. Occasionally plants with

ternate or quaternate leaves are found (e.g., Volcán Antuco, Bío-Bío Prov., Chile, *Solomon* 4435), but this feature does not characterize populations but only sporadic individuals.

Branching is likewise rather variable. Generally stems are simple, or with one or a few lateral branches produced above or from the base. As the growing season progresses, or if the apex of the central shoot is damaged, plants can produce an abundance of lateral shoots throughout. An extreme example of this is shown by a collection from Cautín Prov., Chile (*Solomon* 4537, MO) which was taken from a single plant about 75 cm tall with five major shoots from the base, each with more than 100 lateral branches.

Each erect stem terminates a scaly, branching rhizome that can be up to several decimeters long. Plants of this sort usually appear solitary or in clusters of a few stems. Frequently, however, the rhizomes are tightly and intricately intertwined so that the many shoots are closely spaced with the entire clump producing a rounded, almost shrub-like appearance.

Epilobium glaucum has a broader elevational and latitudinal amplitude than most other species in temperate South America and is often weedy, occupying the same sorts of habitats as the even more widespread and very weedy *E. ciliatum*. In a fashion similar to many other species of *Epilobium*, *E. glaucum* prefers open, permanently moist sites, especially in sand or gravel along mountain streams.

With such an extensive range, it is not surprising that *Epilobium glaucum* grows sympatrically with at least seven other species. Apparent hybrids have been seen between *E. glaucum* and at least four of these, *E. ciliatum*, *E. barbeyanum*, *E. densifolium*, and *E. australe*, which are discussed in detail under each species.

- 11. *Epilobium hirtigerum*** A. Cunn., Ann. Nat. Hist. 3:33. 1839. TYPE: New Zealand, North Auckland, skirts of forest on west side of Wangaroa Harbour, 1833, R. Cunningham (K, holotype; WELT, isotype). *E. junceum* var. *hirtigerum* (A. Cunn.) Curtis, Stud. Fl. Tas. 2:231. 1963. (Complete synonymy given by Raven & Raven, DSIR Bull. 216:141–144. 1976.)

E. tetragonum auct. non L.: Camb. in St.-Hil., Fl. Bras. Merid. 2:192. 1829. Micheli, Fl. Brasil. 13(2):174. 1875, Arechavaleta, Anal. Museo. Nac. Montevideo 5:92. 1905.

E. junceum sensu Hook. f., Fl. N. Z. 1:60. 1853, pro parte.

E. brasiliense Hausskn. Oesterr. Bot. Z. 29:119. 1879. TYPE: Uruguay, Dpto. Montevideo, "Le long de la Riviera qui passe au Moulin des jesuittes de Monte Video," 1767, P. Commerson (P, lectotype, photographs GH, MO; MPU, isolectotype; Raven & Raven, DSIR Bull. 216:141, 1976). Hausskn., Monogr. *Epilobium* 253, tab. 15, f. 71, 71a. 1884. C. Bettfreund, Flora Arg. 230, tab. 140. 1901. H. Lév., Iconogr. *Epilobium*, tab. 190. 1911. Samuelsson, Svensk Bot. Tidskr. 17: 247. 1923. Munz, Comun. Bot. Mus. Hist. Nat. Montevideo 10:25, f. 12. 1943; Fl. Brasilica 41(9): 51, tab. 40. 1947. Cabrera, Fl. Prov. B. Aires 4:321, f. 98. 1965.

E. arechavaetae H. Lév., Bull. Geogr. Bot. 21:149. 1911. TYPE: Uruguay, April–May 1911, J. Arechavaleta. No authentic material has been seen. H. Lév., Cat. Pl. Yun-nan., f. 66. 1916.

E. sarmentaceum sensu Back. & Bakh., Fl. Java 1:262. 1963, non Hausskn., Oesterr. Bot. Z. 29: 149. 1879.

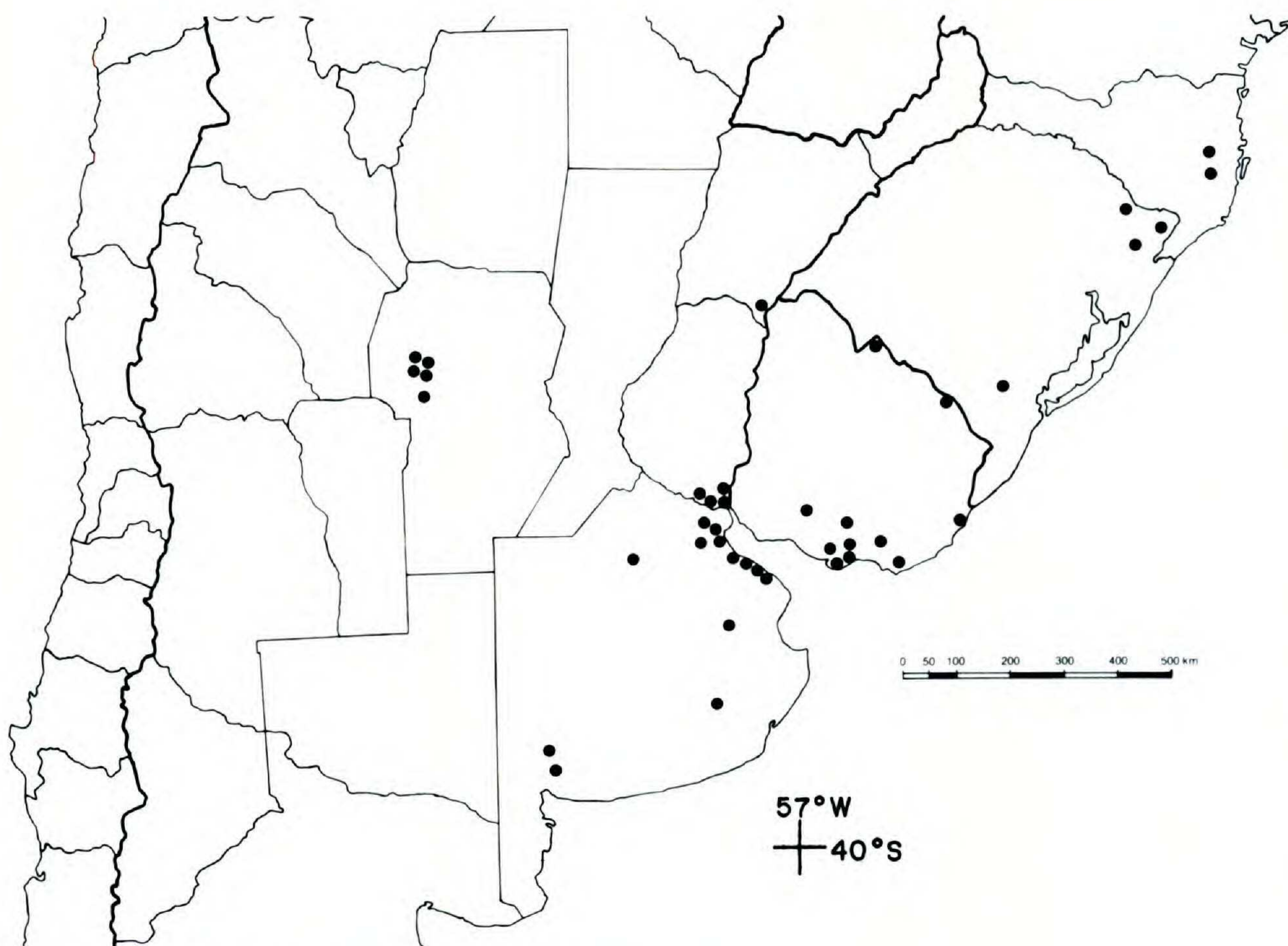
E. cinereum sensu Raven, Blumea 15:273. 1976, non A. Rich., Essai Fl. N. Z. 330. 1832.

Vigorous, perennial herbs, (10–)20–70(–110) cm tall, reproducing vegetatively by elongate leafy shoots from near the base. Stems erect, simple, or branched below, sometimes sparingly branched above, terete, yellow brown or reddish,

somewhat woody with conspicuous exfoliating epidermis at the base, villous throughout, with fine erect hairs 0.25–0.6 mm long, with an admixture of erect glandular hairs 0.1–0.2 mm long. Leaves alternate, only opposite at the first 2 or 3 nodes, thin, bright green, narrowly lanceolate to lanceolate, 1–4.7(–5.6) cm long, 0.2–0.8(–1.3) cm wide, acuminate, rarely the lower acute at the apex, regularly and remotely serrate, with 3–10(–15) forward projecting, slightly hooked teeth, 0.25–1 mm long, on each side, acute to rounded, occasionally clasping at the base, sessile, the adaxial and abaxial surfaces villous and glandular, glabrate with age, then pubescence restricted to the midrib, veins, and margin, the lateral veins inconspicuous, 2–5 on each side of the midrib, sessile. Inflorescence erect, simple. Flowers erect. Ovaries usually densely villous with erect to slightly appressed hairs and erect glandular hairs, 1–2.3 cm long, on pedicels 0–4(–9) mm long. Floral tube 0.4–0.9 mm deep, 1.1–1.6 mm across, externally villous with spreading to appressed hairs and erect glandular hairs, internally with a ring of erect villous hairs, 0.2–0.3 mm long, near the base. Sepals lanceolate, acuminate, 2.5–5 mm long, 0.9–1.2 mm wide, slightly keeled, villous with spreading to appressed and erect glandular hairs. Petals white, obovate, 2.9–4.7 mm long, 1.5–2.8 mm wide, the notch 0.5–0.8 mm deep. Anthers cream, 0.6–0.8 mm long, 0.4–0.6 mm wide; filaments cream, those of the longer stamens 1.2–2.4(–3) mm long, those of the shorter 0.8–1.4 mm long; both sets of anthers shedding directly on the stigma at anthesis and often before the flower opens. Style white, 1.4–2.5 mm long; stigma white, clavate, 0.8–2.3 mm long, 0.4–0.8 mm thick. Capsules erect, villous with spreading to slightly appressed hairs and erect glandular hairs, 2.8–6 cm long, 1.2–1.6 mm thick, on pedicels (0.4–)0.8–2.1 cm long. Seeds brown, papillose, obovoid, 0.8–1 mm long, 0.2–0.4 mm thick, the micropylar end rounded; coma white or slightly yellowish, 4–8 mm long, readily detaching. Gametic chromosome number, $n = 18$.

Distribution (Fig. 11): In Australasia, widely distributed in southeastern Australia, Tasmania, and North Island in New Zealand, rare and scattered on South Island, New Zealand; also in Java and the Lesser Sunda Islands. In South America, found most frequently in marshes and other wet, often disturbed places; in the mountainous parts of its range, most often on moist stream banks and seeps; scattered widely from eastern Santa Catarina and Rio Grande do Sul, Brazil, southward through eastern Uruguay to southern Corrientes, Entre Rios, and Buenos Aires provinces, Argentina, reaching its southern limit in the Sierra de La Ventana (38°S), also in the Sierras Grande and Chica de Córdoba. In the coastal and southern parts of its South American distribution, ranging from near sea level to approximately 200 m, occurring at much greater elevations in the Sierra Grande de Córdoba, 1,300–1,700 m, and the mountains of Santa Catarina and Rio Grande do Sul, 800–1,900 m. Flowering October to February throughout, but not until December in the Sierra Grande de Córdoba.

Representative specimens examined: ARGENTINA, BUENOS AIRES: Chacabuco, 34°38'S, 60°29'W, *without collector in 1923* (LP); Punta Lara, 34°49'S, 57°59'W, *Cabrera 1243* (LP); *Sparre 316* (S); Toloso, 34°53'S, 57°58'W, *Cabrera 7381* (F); Conchitas, 34°47'S, 58°10'W, *Castellanos in 1919* (BA); Tandil, *Castex-Jussen in 1928* (BA); Rosas, 35°58'S, 58°56'W, *Daguerre 194* (BA, MO, RSA); Curramalán, 37°28'S, 62°06'W, *Hauman in 1924* (BAA); Quilmes, 34°44'S, 58°16'W, *Hicken in 1902* (BAF); Delta del Paraná, Arroyo Guazú, *Hicken 1105* (BAF, SI), *Lanfranoli 459* (SI), *Scala 114* (LP, NY); Ituzaingó, 34°40'S, 58°40'W, *Holmberg 120* (SI); Partido Tigre, Las Conchas, *Hunziker 2422* (CORD, LP, SI); Las Palmas, 34°05'S, 59°10'W, *Hunziker 7264* (CORD); Partido Pilar, Río Luján, El Cazador,

FIGURE 11. Distribution of *Epilobium hirtigerum*.

34°25'S, 58°50'W, *Mazzucconi* 713 (BAB); Campana, *Parodi in 1928* (BAA, GH); San Isidro, *Parodi* 10260 (BAA); Villa Elisa, *Pérez-Moreau in 1947* (BA, MO, RSA); Delta del Paraná, Mini, *Burkart* 4031 (BAA, MO), *Scala* 305 (LP, NY); Río Carabelas, 34°15'S, 58°43'W, *Scala in 1925* (NY); Sierra de la Ventana, *Spegazzini in 1895* (LP); La Plata, Isla Santiago, *Spegazzini in 1903* (BAB). CÓRDOBA: Valle de Los Reartes, 31°55'S, 64°34'W, *Castellanos in 1919* (UC); Sierra Achala, cuesta de la Sala Grande, *Hieronymus* 856 (GOET); Dpto. Punilla, Sierra Grande, cerca del Río Yuspe, detrás del Cerro Blanco, 1,650 m, *Hunziker* 10253 (CORD, MO; mixed with *E. ciliatum*); Dpto. Calamuchita, Río San Miguel, camino a Yacanto, *Krapovickas & Cristóbal* 14675 (C, CTES); Dpto. Punilla, Sierra Chica, Tanticuchi, *Kurtz* 4427 (CORD, DS, G, JE, LP, RSA); Sierra Grande, 3 km above Copina, 1,600 m, 31°50'S, 64°10'W, *Solomon* 4131 (MO); La Cumbrecita, 1,450 m, 31°55'S, 64°15'W, *Solomon* 4212 (MO); Sierra Achala, Despeñaderos, Olmedo, *Stuckert* 10542 (CORD, G), *Stuckert* 10813 (CORD); Dpto. Punilla, Villa García, *Stuckert* 20435 (CORD), 20589 (CORD); Dpto. Cruz del Eje, Sierra de Achala, Pampa de San Luis, *Stuckert* 20842 (CORD). CORRIENTES: Dpto. Monte Caseros, Estancia La Potota, *Nicora* 5111 (BAA, CTES, MO). ENTRE RIOS: Delta del Paraná a Arroyo Martínez, *Boelcke* 989 (BAA, MO); Ibicuy, *Burkart* 3595 (BAA); Pasaje Talavera, 33°53'S, 58°55'W, *Gamero* 1033 (LP); 5 km de Brazo Largo, camino a Gualeguaychú, 33°47'S, 58°36'W, *Gamero* 1347 (LP); Delta del Paraná, Río Seibo, *Burkart* 5122 (BAA, MO), *Cabrera* 1945 (LP, NY), *Hunziker* 4617 (BAB, MO); Dpto. Gualeguaychú, camino a Pt. Yerua, desvío a Nueva Escocia, *Troncoso et al.* 2462 (SI).

BRAZIL, Without locality, *Sello* 3186 (JE). RIO GRANDE DO SUL: Without locality, *Gaudichaud* 3186 (P); Serra dos Tapes, *Lindman* 913 (S, UPS); Bom Jesus, 28°42'S, 50°24'W, *Rambo* 8571 (SP); San Francisco de Paula, Vila Oliva, 800 m, 29°14'S, 50°53'W, *Rambo in 1946* (B, S); Prov. Vacaria, Río das Antas, 28°30'S, 50°56'W, *Rambo in 1950* (BR, HBR, MO). SANTA CATARINA: Campos dos Padres, 1,900 m, *Reitz* 2608 (HBR, MO, US); Mun. Bom Retiro, between Fazenda Santo Antonio and falls of Río Canoas, Campos dos Padres, 1,400 m, *Smith & Klein* 7833 (B, HBR, MO, NY, RSA, US); Mun. Bom Jardim, Serra Geral, Campo da Serra de Oratorio, 28°22'S, 49°20'W, *Ule* 1464 (CORD, P).

URUGUAY, CANELONES: Dist. Pando, *Herter* 1147d (MO, S); Barra del Arroyo Carrasco, *Legrand* 864 (POM); 865 (POM), 1327 (F), *Munz* 15443 (BH, GH, NY, POM), *Rosengurt* B429 (POM, US); La Floresta, *Osten* 21665 (BAA, BAF, BREM, GH, MO); Arroyo Canelon Chico, *Rosengurt* 715

(RSA). CERRO LARGO: Río Negro y Arroyo Acegua, *Rosengurtt* 853 (RSA). FLORES: Maciel, Paso de Los Membrillos, *Osten* 4307 (G). FLORIDA: Estancia Rincón de Santa Elena, cerca del Arroyo Timote, 33°29'S, 56°03'W, *Krapovickas* 4825 (LIL). Estancia Rincón de Santa Elena, Arroyo Mansavillagia, *Rosengurtt* 5808 (BR, MO, S, WTU). MALDONADO: Piriapolis, 34°54'S, 55°17'W, *Osten* 5704 (CORD, SI). MONTEVIDEO: Montevideo, *Fruchard* 336 (P), *Giberly* 336 (K), *Gibert* (LP). ROCHA: Palmares de Costillos, 25 km N of Costillos, *Bartlett* 21384 (MICH). SAN JOSÉ: Barra Santa Lucia, *Herter* 1147 (F, G, GH, GOET, M, MO, NY, POM, SI, UC, US, Z), *Osten* 4515 (G), *del Puerto* 803 (F); Arroyo San José, 34°10'S, 55°50'W, *Herter* 1147c (Z). The following additional collections of *Epilobium hirtigerum* from Uruguay are cited in Munz (1943). Although these specimens have not been examined, their assignment to *E. hirtigerum* is nearly certain, since that is the only species known to occur in Uruguay. Munz does not indicate the Uruguayan herbaria in which the specimens are deposited, but they are most likely MVFA or MVM. CANELONES: Canelones, *Arechavaleta* in 1897; Canelón Grande, *Berro* 2318; Bañados del Arroyo Carrasco, *Berro* 8791; Carrasco, *Legrand* 1043. CAVALLEJA: Minas, Cerro Penitente, 34°20'S, 55°07'W, *Berro* 5451. RIVERA: Curticeiras, 31°04'S, 55°29'W, *Berro* 4853. SAN JOSÉ: Barra de Santa Lucía, *Chebataroff* 910, *Osten* 4575.

Epilobium hirtigerum can be easily recognized by its fine erect, villous and glandular pubescence, erect white flowers, elongate leafy basal shoots, and mostly alternate coarsely serrate leaves, the teeth relatively large and somewhat forward projecting. These distinctive features make *E. hirtigerum* unlike any other species. *Epilobium ciliatum* is the only other similar species in South America with white flowers.

The first collections of *E. hirtigerum* from the New World were obtained by P. Commerson in 1767 from the vicinity of Montevideo, Uruguay. As has often been the case with early collections of *Epilobium* from outside Europe, they were compared with familiar European species, and, in this case, included under the name of *E. tetragonum*. The inclusion of this distinctive taxon in *E. tetragonum* persisted until the early years of this century, although Haussknecht described the South American populations as a separate species, *E. brasiliense*, in 1879 (Haussknecht, 1879). Most subsequent workers have considered *E. brasiliense* a distinct, endemic species (Samuelsson, 1923, 1930; Munz, 1943, 1947). Only with intensive study of the Australasian species (Raven & Raven, 1976), did it become apparent that *E. brasiliense* is conspecific with the widespread and variable *E. hirtigerum*. (Reference should be made to Raven & Raven (1976) for a detailed discussion of the morphological variation in this species within Australasia.)

All South American populations are characterized by small, white, highly autogamous flowers, as are most populations in Australasia. Functional cleistogamy is very common, since the anthers often shed their pollen directly on the stigma before the flowers open. The most conspicuous variation is in the size and shape of the leaves and the pubescence of the inflorescence and ovaries. The broadest and longest leaves often occur on rather lax, weak-stemmed plants and are probably shade forms, while the smallest-leaved plants are from more open, perhaps drier sites. The majority of populations have dense, erect or slightly appressed pubescence, which gives the inflorescence and ovaries a grayish appearance. A few populations are less densely villous, but all have an abundance of erect glandular hairs.

Epilobium hirtigerum is the only species that occurs in eastern South America, with most of its range in northeastern Argentina, Uruguay, and southern Brazil. Only in the Sierra Grande de Córdoba does it grow sympatrically with any other *Epilobium* species, in this case *E. ciliatum* and *E. denticulatum*. Often all three species grow intermixed along stream banks. Occasional apparent hy-

brids with *E. ciliatum* are known (Pampa de San Luis, *Stuckert* 20842, CORD; and Arroyo del Medio, *Hieronymus* 750, CORD; pollen stainability 28% and 26%, respectively), and are particularly significant since they show that, despite the often cleistogamous flowers, *E. hirtigerum* does hybridize with other species.

12. *Epilobium conjugens* Skottsberg, Wiss. Ergebnisse Schwed. Südpolar-Exp. 4(4):24, *tab. 1, f. 3a–d*. 1906. TYPE: Argentina, Terr. Tierra del Fuego, Ushuaia, Martial Mountains, 810 m, 11 March 1902, *C. Skottsberg* 206 (S, lectotype here designated, photograph MO; BA, S, SI, UP, isoelectotypes). Samuelsson, Svensk Bot. Tidskr. 17:393. 1923.

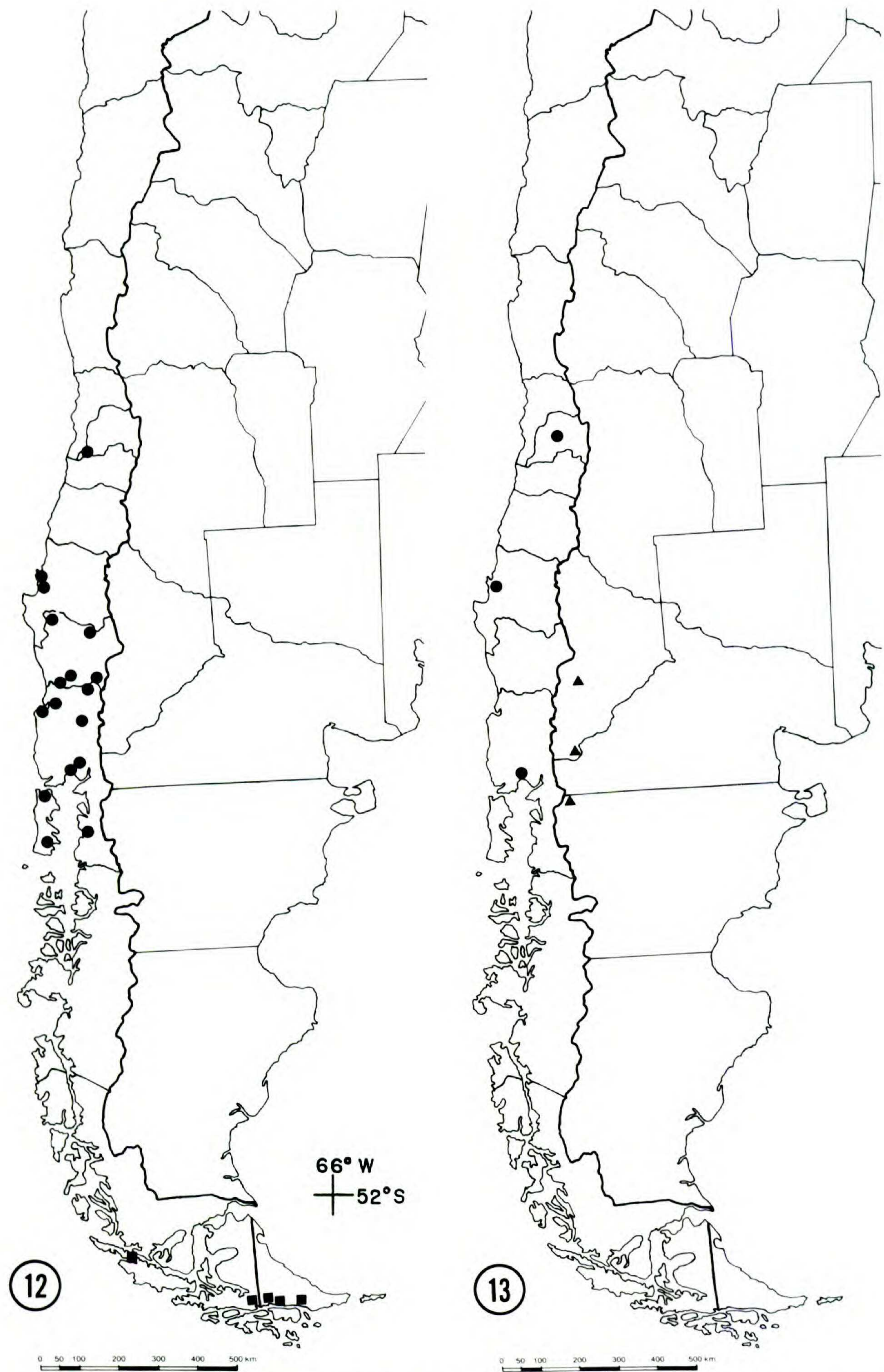
Matted, creeping, perennial herb; stems terete, prostrate, yellowish or pale brown, minutely puberulent, with hairs 0.02–0.08 mm long at the nodes, or glabrous, occasionally in descending lines from the petiole bases, internodes shorter than leaves, giving the plant a congested appearance; the stems continuing to grow and root at the nodes beyond the point where the flowers are produced. Leaves opposite, thick, dull green or sometimes reddish lustrous above, broadly elliptic to rotund or orbicular, 2.5–8.7 mm long, 1.7–6.4 mm wide, broadly obtuse to rounded, occasionally somewhat acute at the apex, entire or with 1–3(–5) obscure teeth on each side, the margin slightly revolute, obtuse, rounded, or occasionally truncate at the base, glabrous, the lateral veins obscure, none or 1, occasionally 2, on each side of the midrib, on winged petioles 1–2.3 mm long, 0.7–1.5 mm wide, merging more or less abruptly with the blade. Flowers erect, solitary and scattered in the middle and upper portions of the stem. Ovaries often reddish, glabrous, 4–6.5 mm long, on pedicels 2.5–5 mm long. Floral tube 0.4–0.7 mm deep, 1.2–2 mm across, externally and internally glabrous. Sepals lanceolate, 3.2–4 mm long, 0.9–1.2 mm wide, glabrous. Petals white to slightly pinkish, obovate, 2.8–4.4 mm long, 2.3–2.8 mm wide, the notch ca. 0.7 mm deep. Anthers cream, 0.36–0.5 mm long, 0.3–0.5 mm wide; filaments cream, those of the longer stamens 0.8–1.2 mm long, those of the shorter 0.6–0.8 mm long; both sets of stamens shedding directly on the stigma at anthesis. Style cream, 1–1.3 mm long; stigma cream, capitate, flat-topped, 0.35–0.6 mm long, 0.4–0.5 mm thick. Capsules erect, glabrous, 1.3–3.5 cm long, 0.9–1.2 mm thick, on pedicels 1–2.2 cm long. Seeds light brown, minutely papillose, narrowly obovoid, 0.7–1.1 mm long, 0.25–0.4 mm thick; coma white to slightly yellowish, 4–6 mm long.

Distribution (Fig. 12): In moist moss mats and other damp places above timberline. Known only from the southernmost mountain ranges of Tierra del Fuego facing the Beagle Channel, and Isla Desolación, at elevations of 400 to 1,000 m. Flowering January to early March.

Specimens examined: ARGENTINA, TIERRA DEL FUEGO: Estancia Harberton, Flat Top Mtn., *Goodall* 1135 (MICH, NA, UC), *Moore* 1391 (BAB, MO); Mountains behind Punta Segunda, E of Mt. Trapezio, *Goodall* 1482 (MICH, MU, NA); Ushuaia, Monte Martial, *Goodall* 4763 (BAB, MO); Sierra Sorondo, 1,000 m, 54°47'S, 67°58'W, *Moore* 1978 (MO); Sierra Sorondo, above Las Cotorras, 750 m, *Santesson* 462 (GB).

CHILE, XII REGIÓN (MAGALLANES): *Antártica Chilena*, Cordón Pirámide, valley E of Yendegaia airfield, 500 m, *Goodall* 3822 (BAB, HIP, LTR, MICH, MO, MU, NA, SI, UC). *Magallanes*, Isla Desolación, Puerto Angosto, 400 m, 53°12'S, 73°22'W, *Dusén* 684 (UPS).

This distinctive South American species is rarely seen or collected due to the inaccessibility of its habitat and very limited geographical range. The creeping



FIGURES 12-13. Distribution of *Epilobium* species.—12. *E. obscurum* (dots); *E. conjungens* (squares).—13. *E. tetragonum* (dots); *E. paniculatum* (triangles).

habit, with the stem produced beyond the flowers and rooting at the nodes, and the suppression of the typical, more or less discrete inflorescence of other species, make it unique among South American species.

From data in Raven & Raven (1976), *Epilobium conjungens* seems most closely related to *E. brunnescens*, a widespread species composed of three subspecies, two throughout New Zealand, and the third endemic in southeastern Australia (West & Raven, 1977). It differs significantly from any of these, however, in being nearly glabrous, with minute hairs only at the junction of the fused petiole bases, rarely with descending lines of scattered hairs, erect flowers with short glabrous pedicels (<5 mm) at anthesis, short fruiting pedicels (<2.2 cm), and the leaves always longer than the internodes.

All of the collections of *Epilobium conjungens* are quite homogeneous. The greatest variation is exhibited by the amount of pubescence and the size and shape of the leaves. *Epilobium conjungens* may grow sympatrically with *E. australe*, as this is the only species that reaches elevations above 400 m within the geographic range of *E. conjungens*, but they are probably separated by habitat preference.

13. ***Epilobium obscurum*** Schreb., Spicil. Fl. Lips. 147, 155. 1771. TYPE: Germany, vicinity of Leipzig. Apparently lost. (Synonymy not given.) Raven, Fl. Europ. 2:310. 1968.

Robust perennial herbs, 40–90 cm tall, reproducing vegetatively and overwintering by elongate leafy shoots produced at or near the base. Stems erect or ascendent, terete or quadrangular, freely branched above and below, becoming reddish purple with age, strigillose with hairs 0.15–0.25 mm long, densely so in the inflorescence, glabrate below and then pubescence restricted to raised descending lines from the decurrent petiole bases. Leaves mostly opposite, alternate above, thin, dull blue green, narrowly lanceolate to lanceolate, or lance-elliptic, 2.5–5 cm long, 0.5–1 cm wide, acute or acuminate at the apex, more or less regularly denticulate with 10–30 teeth on each side, obtuse, or occasionally acute at the base, strigillose on the margins, abaxial midrib, and veins, glabrous adaxially, the lateral veins prominent, impressed above, 4–6 on each side of the midrib, sessile. Inflorescence erect, sparingly branched, the leaves subtending the flowers much reduced in size. Flowers erect. Ovaries often reddish, strigillose, usually densely so, occasionally with erect glandular hairs 0.1–0.15 mm long, 1.5–2.5 cm long, on pedicels 0.6–1.3 cm long. Floral tube occasionally reddish, 0.6–1.2 mm deep, 1.4–2.3 mm across, externally strigillose with a few erect glandular hairs, internally with a ring of erect villous hairs, 0.2–0.3 mm long, near the base. Sepals lanceolate, 2–3.4 mm long, 0.8–1.5 mm wide, slightly keeled at the base, strigillose. Petals rose purple, obovate, 4–5.5(–6.8) mm long, 2–3.2(–4.4) mm wide, the notch 0.8–1.4 mm deep. Anthers cream or yellowish, 0.4–0.9 mm long, 0.4–0.9 mm wide; filaments cream, those of the longer stamens 1.2–2.2 mm long, those of the shorter 0.8–1.3 mm long, the longer stamens, and occasionally the shorter, shedding pollen directly on the stigma at anthesis. Capsules erect, strigillose, 3–6 cm long, 1–1.4 mm thick, on pedicels 0.4–1.5(–2) cm long. Seeds brown, papillose, obovoid, 0.7–0.9 mm long, 0.3–0.4 mm thick; coma white, 4–8 mm long, readily detaching. Gametic chromosome number, $n = 18$.

Distribution (Fig. 12): Throughout Europe, except for much of the European USSR, and the northernmost parts; also in the Azores, Madeira, Canary Islands, locally in Morocco, and the Amanus Mountains of Turkey. Introduced and widely naturalized in New Zealand, and perhaps only recently established in Tasmania (Raven & Raven, 1976). In South America, introduced and widely naturalized in central Chile from Aculeo (Maipo Prov.) to Isla Chiloé, at elevations from near sea level to 1,200 m. Frequent and weedy along roadside ditches, but also occurring in rocky or sandy stream beds, seeps, or other moist, disturbed situations. Flowering November to March.

Specimens examined: CHILE, REGIÓN METROPOLITANA (SANTIAGO): *Maipo*, Aculeo, 33°53'S, 70°53'W, *Bertero* 236 (P). VIII REGIÓN (BÍO-BÍO): *Concepción*, 5 km SE of Concepción, 20 m, 36°50'S, 73°05'W, *Solomon* 4414 (MO); San Pedro, *Suwalsky in 1954* (CONC). XI REGIÓN (ARAUCANÍA): *Cautín*, 2 km E of Villarrica, 200 m, 39°17'S, 72°12'W, *Solomon* 4521 (MO); Termas de Palguín, 700 m, 39°21'S, 71°45'W, *Solomon* 4526 (MO). *Malleco*, 5 km below Vegas Blancas, 600 m, 37°45'S, 72°58'W, *Solomon* 4460 (MO); 3 km below Vegas Blancas, 950 m, 37°45'S, 72°58'W, *Solomon* 4471 (MO); Termas de Tolguaca, 1160 m, 38°15'S, 71°45'W, *Solomon* 4482 (MO). X REGIÓN (LOS LAGOS): *Chiloé*, Lago San Miguel, 43°04'S, 73°40'W, *Marticorena et al.* 106 (CONC); Ancud, 41°52'S, 73°50'W, *Seki* 103 (CONC). *Llanquihue*, 20 km E of Puerto Varas, 50 m, 41°15'S, 72°47'W, *Solomon* 4597 (MO); 5 km E of Puerto Montt, *Wall & Sparre in 1947* (S). *Palena*, Chaitén, *Marticorena* 1693 (CONC). *Valdivia*, La Paz, 39°24'S, 73°44'W, *Eaton in 1976* (MO); Teja Island, 39°50'S, 73°20'W, *Ramírez in 1975* (MO), *Romero in 1966* (VALD); *Santos in 1959* (VALD), *Westermeier in 1973* (VALD); Río Cau-cau, *Schlegel* 6882 (VALD); 1 km W of Coñaripe, 220 m, 39°34'S, 72°00'W, *Solomon* 4540 (MO); Lago Santo Domingo, 8 km SE of Valdivia, 10 m, 39°50'S, 73°10'W, *Solomon* 4558 (MO); Corral, 10 m, 39°50'S, 73°26'W, *Solomon* 4571 (MO); Fundo San Martín, *Woerner in 1953* (CONC, mixed with *E. puberulum*).

This distinctive, primarily European, species can now be found over a large part of central Chile. It is most easily distinguished by the erect glandular hairs that are restricted to the floral tube, the elongate leafy basal shoots, the narrowly lanceolate to elliptic, denticulate leaves, and the rose-purple petals. Commonly it grows in roadside ditches, intermixed with *Epilobium ciliatum*, the species with which it is most likely to be confused. *Epilobium ciliatum*, however, is distinctive in having ridged seeds with a chalazal appendage, leafy basal rosettes or turions, glandular hairs present throughout the inflorescence, and white or pale pink petals. In New Zealand there has been great confusion between *E. ciliatum* and *E. obscurum*. Petrie, in fact, described a new native species, *E. erectum*, based on a mixed collection of these two species (Raven & Raven, 1976). Only rarely was *E. obscurum* observed growing sympatrically with *E. glaucum* (Near Coñaripe, Lago Calafquén, Prov. Valdivia) or *E. puberulum* (Fundo San Martín, Prov. Valdivia), both of which are sometimes weedy.

Epilobium obscurum was first collected in Chile at Aculeo (Prov. Maipo) in March 1828 (*Bertero* 236, P). The next collections were not made until 1947 (*Wall & Sparre*, S) at Puerto Montt. Apparently no one has previously recognized this species or recorded it from South America. Steudel did base *E. hispidulum* (nomen nudum) on *Bertero's* collection, but this name passed rapidly into oblivion (Steudel, 1840).

All of the available collections of *Epilobium obscurum* are relatively uniform in habit, leaf shape, pubescence, etc., the only exception being a specimen with unusually large flowers (petals 6.8 mm long) from Puerto Montt (*Wall & Sparre in 1947*).

The frequency of *E. obscurum* in the field today, and the lack of any collec-

tions during the latter part of the nineteenth or early twentieth century when a great deal of botanical work was being conducted in central Chile, leads one to surmise that *E. obscurum* may have been introduced more than once, and that any nineteenth century introductions did not persist, or did so only marginally. In fact, *E. obscurum* has not been re-collected in the vicinity of Aculeo since Bertero's time, thus making the northernmost known locality for a recent collection from near Concepción (Suwalsky in 1954, CONC-18972), about 350 km farther south. It is certainly possible that heavy disturbance of the forest regions, and extensive road construction during the past 30 years have allowed the rapid dispersal of *E. obscurum* into areas that were formerly relatively remote, accounting for its apparent explosive spread in recent years.

A probable hybrid between *Epilobium obscurum* and *E. ciliatum* was collected 2.8 km below Vegas Blancas, near Parque Nacional Nahuelbuta (Prov. Malleco, Solomon 4471, MO), where both species were common in and around a swampy pasture. Its hybrid nature is indicated by the presence of erect glandular hairs throughout the inflorescence, the broader, more strongly toothed leaves, the presence of what appear to be turion scales at the base of the plant, poor capsule development, and low seed set. The pollen fertility of this specimen is 26%, a figure that is characteristic of crosses between species with the BB and AA chromosomal arrangement.

14. *Epilobium tetragonum* subsp. *lamyi* (F. Schultz) Nyman, Consp. Flor. Eur. 247. 1879. *E. lamyi* F. Schultz, Flora 27:806. 1844. TYPE: France, "Solo argilloso in arvis humidis prope Limoges," P. Lamy. Type material not seen. (Complete synonymy not given.) Samuelsson, Svensk Bot. Tidskr. 29:9. 1930. Raven, Fl. Europ. 2:30. 1968.

Clumped perennial herbs, 20–100 cm tall, overwintering and reproducing vegetatively by leafy rosettes produced at the base late in the season. Stems erect, branched above, terete or quadrangular, strigillose all around in the upper portions and usually below, or glabrate below, with raised descending lines from the decurrent petiole bases. Leaves mostly opposite, alternate in the inflorescence, thin, dark blue green, often reddish, especially below, lanceolate to oblong-lanceolate, 2.5–5 cm long, 0.5–1.5 cm wide, acute to acuminate at the apex, regularly serrulate with 5–20 teeth on each half, acute to rounded at the base, strigillose on the adaxial and abaxial midribs, veins, and margins, lateral veins prominent, 3–5 on each side of the midrib, on poorly defined petioles 0.5–2 mm long. Inflorescence erect, branched, the leaves subtending the flowers reduced in size. Flowers erect. Ovaries densely strigillose, 1.5–3 cm long, on pedicels 0.3–1.5 cm long. Floral tube 0.8–1.2 mm deep, 1–1.4 mm across, externally strigillose, internally with a ring of erect villous hairs 0.2–0.3 mm long. Sepals lanceolate, 2.5–4 mm long, 0.9–1.3 mm wide, slightly keeled, strigillose. Petals rose purple, obovate, 2.5–5 mm long, 2.1–3.5 mm wide, the notch 1–1.6 mm deep. Anthers yellow, 0.6–1.1 mm long, 0.4–0.6 mm wide; filaments rose purple, those of the longer stamens 1.4–2.5 mm long, those of the shorter 0.7–1.4 mm long, the longer stamens, and occasionally the shorter, shedding pollen directly on the stigma at anthesis. Style white or slightly purplish at the base, 1.5–3 mm long; stigma white,

clavate, 1.4–2 mm long, 0.6–1.1 mm thick. Capsules erect, strigillose, 5–9 cm long, 1–1.6 mm thick, on pedicels 0.5–2 cm long. Seeds brown, coarsely papillose, obovoid, 0.7–1.2 mm long, 0.35–0.5 mm thick, the micropylar end rounded; coma white, 4–7 mm long, readily detaching.

Distribution (Fig. 13): Throughout Europe, southwestern Asia, and North Africa; perhaps introduced, but now widely distributed in South Africa; introduced in New Zealand, where it is rapidly becoming naturalized, and sparingly in Australia and North America. Known as an introduction in South America only from Chile, where it is a rare, and perhaps persistent garden weed in a few cities. Flowering November to January.

Specimens examined: CHILE, REGIÓN METROPOLITANA (SANTIAGO): *Santiago*, Santiago, *Claude-Joseph* 931 (US); Nuñoa, Barrio de Santiago, *Claude-Joseph* 1245 (US). VIII REGIÓN (BÍO-BÍO): *Concepción*, Concepción, *Oehrens* in 1978 (CONC, MO). X REGIÓN (LOS LAGOS): *Llanquihue*, Puerto Montt, *Pfister* in 1942 (CONC).

Epilobium tetragonum subsp. *lamyi* has been collected only four times during the period from 1919 to 1978, twice in Santiago, and once each in Concepción and Puerto Montt. The two collections from Santiago are so similar to each other morphologically that they may have been derived from the same source, although they were collected two years apart. This entity is certainly rare in South America. Its widely scattered occurrence as a garden or street weed in cities might be the result of several introductions, perhaps by contaminated garden seeds from Europe, or some other unknown European source.

The specimens from Chile have all been retained in *Epilobium tetragonum* subsp. *lamyi*, based on the short-petiolate upper leaves and the usually oblong-lanceolate to lanceolate leaf shape (Raven, 1968; Clapham et al., 1962). There is considerable question as to whether or not *E. tetragonum* subsp. *lamyi* should be considered taxonomically distinct from *E. tetragonum* subsp. *tetragonum* (Raven, pers. comm.). Only additional, more detailed studies of this variable species in its native area will be able to resolve this problem.

Epilobium tetragonum subsp. *lamyi* can be distinguished from *E. obscurum* by its leafy basal rosettes, serrulate leaves, and lack of glandular pubescence on the floral tube, and from *E. ciliatum* by its papillose seeds, rose purple flowers, and lack of glandular hairs.

- 15. *Epilobium paniculatum*** Nutt. ex Torr. & Gray, Fl. N. Amer. 1:490. 1840. nom. conserv. prop. TYPE: Oregon, "Rocky Mountains and the Columbia plains," 1834–35, *T. Nuttall* (NY, lectotype; BM, GH 2 sheets, PH, isolecotypes; W. Jepson, Fl. Calif. 2:571. 1936). (Complete synonymy not given.) Munz, N. Amer. Fl. II. 5:207. 1965.

E. brachycarpum Presl, Reliquiae Haenkeanae 2:30. 1831, non Leight., Ann. Nat. Hist. 8:401. 1841; nec sensu Munz, Aliso 4:489. 1960; N. Amer. Fl. II. 5:219. 1965. Nom. prop. rejic., Hoch & Raven (1981a). TYPE: "Mexico," most likely California, Monterey Co., Monterey, 13–23 September 1791, *T. Haenke* (PR, holotype). This is the only locality within the known distribution of *E. paniculatum* where the Malaspina Expedition stopped.

The following description is based on South American plants only: Erect annual herb, 30–60 cm tall, with a long tap root. Stems branched above, terete, glabrous, often somewhat woody at the base, with conspicuously exfoliating epidermis. Leaves mostly alternate, only a few lower nodes opposite, gradually

reduced upwards, with fascicles of small leaves in the axils, often early deciduous, dull green, sometimes slightly glaucous, thick, linear to narrowly lanceolate, 1–3.5 cm long, 2–4.5 mm wide, often conduplicate, acuminate at the apex, remotely denticulate with 3–10 teeth on each side, acuminate at the base, glabrous, the lateral veins apparently absent, on poorly defined petioles 0–3 mm long. Inflorescence erect, paniculately branched, the branches thin, the leaves subtending the flowers reduced to subulate bracts, and fused to the base of the pedicel for 1 to 2 mm. Flowers erect. Ovaries with erect glandular hairs, 0.1–0.5 mm long, or glabrous, 0.9–1.6 cm long, the pedicels glandular pubescent or glabrous, 1–6 mm long. Floral tube reddish, 1.6–2.4 mm deep, 1.2–1.6 mm across, externally glandular pubescent or glabrous, internally with a ring of erect villous hairs ca. 0.1 mm long near the base. Sepals reddish, glabrous, lanceolate, 2–2.7 mm long, 0.8–1 mm wide. Petals rose purple, obovate, 3–4 mm long, 1.2–2 mm wide, the notch 0.5–1.9 mm deep. Anthers cream, 0.8–1 mm long, 0.4–0.5 mm wide; filaments cream, those of the longer stamens 1–1.2 mm long, those of the shorter 0.5–0.8 mm long, the longer stamens shedding pollen directly on the stigma at anthesis. Style cream, 1.8–2.7 mm long; stigma cream, long clavate to capitate, 0.4–1.2 mm long, 0.4–0.5 mm thick. Capsules erect, glandular pubescent or glabrous, 1.9–3.2 cm long, 1.3–1.7 mm thick, on pedicels 3–9 mm long. Seeds mottled gray brown, finely papillose, broadly obovoid, 1.4–1.6 mm long, 0.7–0.8 mm thick, with a conspicuous constriction of the micropylar end 0.3–0.45 mm long; coma white to yellowish brown, 5–7 mm long, readily detaching. Gametic chromosome number, $n = 12$.

Distribution (Fig. 13): Throughout much of western North America from British Columbia to Saskatchewan, North and South Dakota, south to Arizona and New Mexico. Introduced in Argentina, from southwestern Neuquén, south to northwestern Chubut. Open, dry, often disturbed ground. Flowering January to February.

Specimens examined: ARGENTINA, CHUBUT: Between El Bolsón and Leleque, Zöllner 7646 (MO, NA). NEUQUÉN: Dpto. Aluminé, Aluminé, Crespo & Giangualani 2006 (BAB, MO); Dpto. Los Lagos, Valle Encantado, Rio Limay, 40°44'S, 71°07'W, Crespo et al. 2306 (BAB, MO).

The introduced *Epilobium paniculatum* is the only member of the monotypic section *Xerolobium* of western North America. It is easily distinguished from all other South American species by its often conduplicate, early deciduous, glabrous, alternate leaves, the relatively large seeds with a conspicuous micropylar constriction, simple tap root, and annual habit.

The three known South American populations are quite uniform in morphology and habit. They all have simple, clavate or capitate stigmas and small flowers, a widespread feature in North American populations, although other North American populations are characterized by 4-lobed stigmas and much larger flowers (Raven et al., 1981). The most striking morphological variation is in the presence or absence of erect glandular hairs. Plants may be either glabrous, and with hairs only on the pedicels, ovaries, and floral tube. Glabrous or pubescent individuals can be found in the same population (Zöllner 7646), so the absence of hairs may be under a simple genetic control.

This distinctive addition to the introduced flora of Argentina was first collected in 1974 between El Bolsón and Leleque, Chubut Prov. (Zöllner 7646), and reported by Seavey & Raven (1977c). Since then, it has been collected twice,

increasing its range northward to Aluminé, Neuquén Prov., a distance of 300 km. Undoubtedly this species will continue to expand its range in the semi-arid and montane habitats of western Patagonia.

EXCLUDED NAMES

Epilobium lineare Larrañaga, Escritos de D. A. Larrañaga 1:25. 1922 (Publ. Inst. Hist. Geog. Uruguay), non Muhlenberg, Cat. 39. 1813. The plants are described as having yellowish flowers and linear leaves. Yellow or cream flowers are unknown in *Epilobium*, except for *E. luteum*, a North American species. This species is probably a member of the Cruciferae.

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